WORKING PAPER 47

Factors Influencing the Density of Natural Regeneration in Uniform Shelterwoods Dominated by Douglas-fir in the Sub-Boreal Spruce Zone

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Factors Influencing the Density of Natural Regeneration in Uniform Shelterwoods Dominated by Douglas-fir in the Sub-Boreal Spruce Zone

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Three replicates of a uniform shelterwood trial were established in even-aged stands dominated by Douglas-fir in the SBSdw1 variant northeast of Williams Lake, B.C., with initial harvesting conducted in the summer of 1991. Treatments consisted of a two-stage shelterwood leaving 50% residual basal area (RBA) after the first entry and a three-stage shelterwood leaving 70% RBA, with overstory thinning achieved by hand-falling or by feller-buncher. Treatment units were 1.4 ha in area, with an uncut control (100% RBA) at each site. Seedfall was monitored using ten 0.37 m^2 seedfall traps in each treatment unit, inspected twice a year from 1992 through 1998. The abundance of different ground surface materials was surveyed in 1990, 1991, and 1993. Controlled germination experiments were conducted in 1994, 1995, and 1996 on four seedbed materials (forest floor, live moss, rotting wood, and mineral soil) across all RBA levels. Surveys of the density of natural regeneration were conducted in 1990, 1991, 1993, 1994, and 1996.

Seed rain density varied considerably from year to year, peaking in 1993 and 1995 for Douglas-fir, and in 1993 and 1994 for hybrid white spruce. Differences among harvesting treatments were marginal, with some indication that Douglas-fir seed production was enhanced in the heavy removal treatment, at least in 1995. Seed predation by animals likewise varied considerably from year to year, though it was relatively uniform among treatments (approximately 2.4–3.3% per day). Douglas-fir seed consumption was significantly greater in the partially cut treatments than in uncut stands. This habitat effect was especially evident in late summer and early autumn (when rodent populations are higher). Cumulative annual Douglas-fir seed losses over autumn and winter were estimated to range from 70.8 to 99.6% in different treatment units in different years.

Even after logging, seedbeds were dominated by organic forest floor materials. Live moss cover was destroyed in proportion to the basal area of timber removed. Logging operations increased the exposure of mineral soil from levels of 0.4% up to approximately 2.2% cover, and of rotting wood from 2 to 6% cover. Since harvesting activities also increased the prevalence of fine woody debris (logging slash) on the ground, they did not necessarily increase the net availability of microsites suitable for tree seed germination in the short term.

Douglas-fir, hybrid white spruce, lodgepole pine, and subalpine fir all exhibited their best germination on rotting wood, followed by mineral soil, intact forest floor, and live moss mats. The first-year survival of new seedlings likewise was greatest on rotting wood and mineral soil, with the poorest germinant survival on moss mats. Survival of spruce and pine germinants on intact forest floor was intermediate, but Douglas-fir and subalpine fir germinant survival on intact forest floor did not differ significantly from that observed on rotting wood and mineral soil. Germination and early survival on organic seedbeds was negatively correlated with high light availability and with moisture stress near the surface.

Repeated regeneration surveys suggest that some of the original advance regeneration, growing in scattered clusters, died during harvesting. A flush of seedlings (primarily Douglas-fir) was observed in 1994, following the large seed crop produced in 1993. Regeneration densities declined somewhat from 1994 to 1996, though proportional losses did not differ significantly among

treatments. Subcanopy light measurements in harvested plots averaged only 13–23% relative irradiance, suggesting that conditions are still sub-optimal for conifer regeneration. Five years after harvesting, the relative abundance of seedlings in different treatment units remains similar to their rank prior to logging. The factors that determine the abundance of natural regeneration can be summarized in a simple model that starts with empirical estimates of seedfall densities for the previous year. Seed densities are then depleted according to habitat-specific seed predation levels, and the remainder are multiplied by the germination and germinant survival rates observed on different seedbeds, weighted by the abundance of each seedbed type.

All treatments were successful in producing dense new Douglas-fir regeneration (1533–30 433 stems/ha) and in protecting them from growing-season frosts. No significant differences in the density of all Douglas-fir regeneration, or seedlings established since logging, were observed among the four alternative treatments and the uncut control during the first 5 years after logging. Treatments with 50% RBA and those logged by feller-buncher supported significantly higher densities of some categories of regeneration. Continued monitoring is needed to evaluate these treatments further, and results will change after the seed cut (second entry) is implemented in 2001 for the 70% RBA treatment. Results to date suggest that a low residual basal area, combined with a high level of forest floor disturbance, is preferable for enhancing conifer regeneration. It is tentatively recommended that a preparatory cut is not necessary for naturally regenerating Douglas-fir under a shelterwood overstory in this zone, and that the seed cut should leave less than 50% residual basal area.

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CONTENTS

Summary iii

Acknowledgements iv

1. Introduction 1
   1.1 Background 1
   1.2 Objectives 2

2. Methods 3
   2.1 Study Area 3
   2.2 Stand Treatments 3
   2.3 Stand Structure Assessment 6
   2.4 Microclimate Monitoring 6
   2.5 Seed Rain 7
   2.6 Seed Predation 7
   2.7 Seedbed Distribution 8
   2.8 Seed Germination and Germinant Survival 8
   2.9 Natural Regeneration Density 10
   2.10 Growth of Natural Regeneration 11
   2.11 Statistical Analysis 11
   2.12 Synthesis 13

3. Results 15
   3.1 Stand Structure after Harvest 15
   3.2 Weather and Microclimate 16
   3.3 Seed Rain 20
   3.4 Seed Predation 22
   3.5 Seedbed Distribution 24
   3.6 Seed Germination 27
   3.7 Germinant Survival 29
   3.8 Natural Regeneration Densities 31
   3.9 Growth of Natural Regeneration 41
   3.10 Synthesis 42

4. Discussion 46
   4.1 Seed Rain 46
   4.2 Seed Predation 47
   4.3 Seedbed Distribution 47
   4.4 Seed Germination 48
   4.5 Germinant Survival 49
   4.6 Regeneration Densities 49
   4.7 Synthesis 51
   4.8 Management Implications 51
   4.9 Suggestions for Further Study 52

5. Conclusions 54

Literature Cited 55

APPENDICES

1 Partitioning of variance associated with germination and germinant survival 59
2 Regeneration densities estimated from frequency classes 61
3 Summarized Douglas-fir regeneration and environmental data used in correlation and simulation modelling 63

TABLES

1 Sampling details and size class definitions used in regeneration sampling 10
2 Basal area and volume of standing trees prior to harvest, immediately after harvest, and after salvage operations had removed windthrown trees and those subject to bark beetle infestation 16
3 Mean growing season environmental conditions experienced under different stand treatments at the Beedy Creek site, 1991–1995 19
4 Estimated densities of mature or viable seeds summarized over all three locations from 1992 to 1997 21
5 Percent cover of different seedbed materials assessed during regeneration surveys in 1993, analyzed for treatment effects across all three locations 26
6 Summary of 1990 regeneration frequency per 30 sample plots 32
7 Contingency table analysis of the frequency of six classes of regeneration density observed under the five different treatments and three locations in 1990 33
8 Summary of 1991 regeneration frequency per 30 plots 34
9 Contingency table analysis of the frequency of six classes of regeneration density observed under the five different treatments and three locations in 1991 35
10 Regeneration densities in 1993, Year 2 post-treatment, comparing treatments across all three locations 36
11 Regeneration densities in 1994, Year 3 post-treatment, comparing treatments across all three locations 37
12 Regeneration densities in 1996, Year 5 post-treatment, comparing treatments across all three locations 38
13 Retrospective growth analysis on natural regeneration conducted in 1994 42
14 Significant results of correlation analysis among Douglas-fir regeneration variables and environmental attributes 43
15 Evaluation of model predictions, given the uncertainty in both the surveyed and modelled data 45
A1.1 Partitioning of variance and significance of substrate and removal effects on seed germination 59
A1.2 Partitioning of variance and significance of substrate and removal effects on the first-year survival of newly germinated tree seedlings 60
A2.1 Regeneration densities in 1990, estimated from density classes 61
A2.2 Regeneration densities in 1991, estimated from density classes 62
A3.1 Regeneration and environmental values used for correlation and multiple regression analysis, Douglas-fir, 1993, 1994, and 1996 63

A3.2 Summary of parameters influencing the natural regeneration of Douglas-fir over 3 years and their resulting predictions for germinant densities 64

FIGURES

1 Location of study sites and treatment units at each site 5
2 Conceptual model of natural regeneration in partially cut stands 14
3 Average stand structure of canopy trees at the three study sites, summarized for (a) pre-harvest conditions, (b) 70% residual basal area treatment units, and (c) 50% residual basal area treatment units 17
4 Partial climate diagram derived for the Beedy Creek site 18
5 Input of viable Douglas-fir seeds over time, for each of three canopy removal treatments, all three locations combined 21
6 Mean densities of viable Douglas-fir seeds at each location, all treatments combined 22
7 Relationship of percent viable seed to the size of the annual seed crop in Douglas-fir 23
8 Mean rates of Douglas-fir seed loss to small mammals under each cutting treatment in each of 4 years, all three locations combined 23
9 Seasonal trends in seed predation under different residual basal area treatments 24
10 Occurrence of suitable seedbeds—(a) disturbed duff or moss, (b) rotting wood, and (c) mineral soil—under different stand treatments in 1991 and 1993 25
11 Abundance of general seedbed categories in autumn 1993, all years and locations combined 26
12 Year-to-year differences in overall germination by each tree species, all stand treatments, seedbeds, and locations combined 27
13 Mean germination of each tree species on different seedbeds, averaged over all years, locations, and stand treatments 28
14 Mean germination of Douglas-fir on different seedbeds under different canopy removal treatments, all locations and years combined 28
15 Year-to-year differences in overall first-year survival of newly germinated seedlings of each species tested, all seedbeds and stand treatments combined 29
16 Mean first-year survival of new germinants of each tree species on different seedbeds, all stand treatments, locations, and years combined 30
17 Mean first-year survival of germinants under different canopy treatments, all years and locations combined 30
18 Mean first-year survival of Douglas-fir germinants on different seedbeds under different canopy treatments, all years and locations combined 31
19 Trends in estimated Douglas-fir regeneration density over 7 years, all size classes and locations combined 39
20 Trends in estimated hybrid white spruce regeneration density over 7 years, all size classes and locations combined 40
21 Trends in estimated subalpine fir regeneration density over 7 years, all size classes and locations combined 40
22 Estimated densities of Douglas-fir seedlings likely to have germinated since harvesting in 1991, all locations combined 41

23 Observed densities of Douglas-fir germinants in 1993, 1994, and 1996 compared to model predictions 46

1.1 Background

Artificial regeneration of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) has frequently been unsuccessful in clearcuts in the dry warm subzone of the Sub-Boreal Spruce biogeoclimatic zone (SBSdw) (Steen et al. 1990). This subzone is characterized by a warm, dry summer climate and frequent frosts during the growing season (Meidinger et al. 1991). These summer frosts can be especially severe in depressions and on lower slopes where cold air drainage accumulates (Steen et al. 1990). Douglas-fir is one of the least frost-tolerant species in the Sub-Boreal Spruce zone, where it reaches the northern limits of its natural range (Minore 1979; Klinka et al. 1998). Significant frost damage to Douglas-fir seedlings has been observed in plantations through much of the Cariboo Forest Region. In the adjacent Interior Douglas-fir (IDF) biogeoclimatic zone, Douglas-fir has been harvested using selection systems for several years (Weetman and Vyse 1990). The residual canopy provides shade and frost protection, thereby ensuring successful Douglas-fir regeneration. Unlike in the IDF zone, Douglas-fir stands in the SBSdw subzone are generally even-aged and occur in mixture with other species. In much of this subzone, large tracts of forest successfully regenerated after widespread fires in the mid-1800s.

Because of the problems establishing Douglas-fir in clearcuts, lodgepole pine (*Pinus contorta* var. *contorta*) is the predominant species planted in this subzone, even when Douglas-fir was the dominant species in the original stand. Lodgepole pine is generally not as productive (in terms of site index) as Douglas-fir on these sites (B.C. Ministry of Forests 1997), and its widespread introduction as a crop tree compromises tree species diversity at the stand and landscape levels. The SBSdw subzone is widespread in central British Columbia, and is close to population centres (including Williams Lake, Quesnel, Prince George, Vanderhoof, and Fort St. James), and the forest is a valuable resource for many non-timber uses: range, wildlife, recreation, and water supply. There is currently tremendous public pressure to reduce the use of clearcut harvesting not only in the Sub-Boreal Spruce zone, but throughout the Cariboo Forest Region and throughout the province.

In response to these issues, use of the uniform shelterwood system (Matthews 1989) has been suggested as a means of providing suitable environmental conditions for Douglas-fir regeneration in this climate, while also addressing numerous aesthetic and other non-timber concerns. As early as 1978, approximately 162 000 ha of National Forest land in the Pacific Northwest of the United States had been treated by shelterwood cutting in response to similar concerns in the 1960s and 1970s (Hughes 1979). Shelterwood silvicultural systems encourage even-aged crop development, as in clearcutting systems, but with a thinned overstory retained to provide tree seeds (thereby facilitating natural regeneration) and partial shade until the stand becomes fully stocked with the next crop. Mature trees can be removed in regular or irregular clumps (gaps), in strips, or individually on a uniform basis throughout the stand. Shelterwood harvesting consists of at least two entries: an initial "seed cut" to open the canopy and disturb the seedbed sufficiently to stimulate regeneration, followed by a "removal cut" to later harvest the residual trees once the regeneration is well established and able to withstand an open environment, which may take up to 30 years. Sometimes three or more harvest entries are employed: a "preparatory cut" may precede

the seed cut to increase tree vigour, windfirmness, and seed production (Nyland 1996), though Matthews (1989) questions the effectiveness of such preparatory fellings. Another optional "secondary cut" may also precede the final removal cut in order to open the canopy gradually, thereby giving the regenerating crop more time to adapt to open conditions (Matthews 1989).

All shelterwood systems retain a relatively high density of overstory trees for seed production and shade generation until the new crop is well established. Additional protection from radiation frosts can often be achieved under uniform shelterwoods (Tesch and Mann 1991) because the sky view factor near the forest floor is never as great as it is in multi-tree gaps or in clearcuts. Partial cutting according to a shelterwood prescription can leave a stand looking relatively undisturbed, thereby meeting visual quality objectives as well. Developing an appropriate shelterwood system for application in a previously untried forest type requires the evaluation of several alternatives, including the number of entries (fellings), the timing of each entry, the degree of canopy thinning at each entry, and the degree of forest floor disturbance required to meet regeneration goals and other objectives.

1.2 Objectives

This study was initiated and established as a cooperative effort of Weldwood of Canada Ltd., the University of British Columbia (UBC) Alex Fraser Research Forest, and the Research Section of the B.C. Ministry of Forests in the Cariboo Forest Region. Started in 1989, this operational field trial was designed to assess the applicability of a uniform shelterwood system for mixed-conifer forests dominated by Douglas-fir in the SBSdw subzone. Emphasis was placed on the monitoring of windfirmness and Douglas-fir regeneration success when manipulating the number of harvest entries (or the intensity of each cut) and the harvesting methods employed. Factors known to influence the establishment of Douglas-fir seedlings (such as microclimate conditions, seedfall density, seed predation, seedbed distributions, duff thickness, and vegetation response) were assessed.

This report describes those components of the study related to the density of natural regeneration observed under alternative treatments during the first 8 years of the project (1990–1997). In particular, it is the purpose of this document to describe and test for significant differences among treatments in the following attributes, especially as they relate to Douglas-fir regeneration:

1. density of viable seed rain
2. seed losses due to predation by rodents
3. relative abundance of different seedbeds
4. germination on different seedbeds
5. early seedling survival on different seedbeds
6. densities of natural regeneration in different size classes
7. agreement between predicted (from components 1, 2, 3, 4, and 5) and observed (component 6) densities of natural regeneration

Other attributes monitored during the study but not directly related to regeneration density (e.g., microclimate, non-crop vegetation, quality and vigour of seedlings, performance of planted seedlings) are reported here only insofar as they influence or help interpret observed densities of natural regeneration.

2.1 Study Area

Three sites were chosen in the Horsefly variant of the dry warm Sub-Boreal Spruce subzone (SBSdw1) north and northeast of Williams Lake for treatment replication (Figure 1). Each site was selected for uniformity of topography and ecological characteristics (i.e., soil nutrient regime and soil moisture regime), and for species composition and stand age. Selected stands were 80–120 years old and were comprised of a mix of Douglas-fir and lodgepole pine, with Douglas-fir always the dominant species. Soils and site characteristics were described for each treatment unit on each site, and each unit was classified to site series.

The Beedy Creek location (referred to as "Skelton Valley" by von Trebra et al. 1998) is 45 km north of Williams Lake in the Williams Lake Forest District. It is situated on a zonal falsebox-sarsaparilla site series (mesic soil moisture regime, medium-rich soil nutrient regime) of the SBSdw1 variant (B.C. Ministry of Forests 1989). The site has a west-facing aspect and is located midslope at approximately 800 m elevation. Soils are moderately well-drained luvisols with a mor humus form. Douglas-fir comprised approximately 65% of the total volume prior to harvest.

The Gavin Road site is located in the Horsefly Forest District, 45 km northeast of Williams Lake, on the middle to upper portion of a south-facing slope at an elevation of 1050 m. It is also characterized as a zonal falsebox-sarsaparilla ecosystem and has soils similar to those described at the Beedy Creek site. Douglas-fir made up approximately 83% of the total volume prior to harvest.

The UBC Forest site is located on the Alex Fraser Research Forest in the Horsefly Forest District, just 1.6 km south of the Gavin Road location. This site, too, is on a zonal site unit (falsebox-sarsaparilla ecosystem), on flat terrain, and at approximately 1050 m elevation. Soils are similar to those found on the other two sites. Douglas-fir made up approximately 67% of the total timber volume. More hybrid white spruce (*Picea engelmannii* × *glauca*) was present on this site than on the others, perhaps indicating a slightly wetter soil moisture regime.

2.2 Stand Treatments

The silvicultural systems being investigated are variants of a uniform shelterwood, designed to compare a two-entry approach with a three-entry approach, and to compare the efficacy of hand-falling with that of a mechanical feller-buncher. This report discusses results obtained in the 6–7 years after the first entry only.

The two-entry treatment was designed to remove 50% of the stand's basal area in the seed cut and the remainder in the removal cut. The three-entry treatment was designed to remove 30% of the basal area in a preparatory cut, to be followed by 20–30% removal in the seed cut, and the remainder in the removal cut. Though the preparatory cut in the treatment units scheduled for three entries was not necessarily intended to induce regeneration at this time, these units were fully monitored for seedbed attributes and natural regeneration as well. If high densities of seedlings were found to establish after this light cutting, then the next entry could be a "secondary cut" rather than a seed cut. To better portray the environmental conditions in each plot along a continuum of canopy opening, and to put these treatments in the context of variable retention harvesting (Franklin et al. 1997), we hereafter

refer to the timber removal treatments in terms of the nominal basal area remaining; that is, 50, 70, or 100% residual basal area (RBA). Some components of the study involve comparisons to 0% RBA (clearcut) sites, which were created nearby at approximately the same time as the study was initiated, but not formally part of this project's experimental design.

Each cutting treatment was implemented using either hand-falling (HF) or a feller-buncher (FB) in different treatment units in order to compare the economic and silvicultural effectiveness of these alternative harvesting techniques. Because the feller-buncher laid each bole directly onto trails for skidding, while the hand-felled boles were skidded from their point of falling, it was hypothesized that more suitable seedbeds would be exposed by hand-falling with line skidding.

Five treatment units measuring 100 × 140 m each (1.4 ha) were established on each site, with 20-m buffers between units (Figure 1). A buffer up to 100 m wide was also established around the outside perimeter of each trial site. The five alternative treatments were randomly assigned to a treatment unit at each of the three locations, which serve as statistical blocks. Treatments were:

1. 100% RBA — control with no harvesting, 100% residual basal area (approximately 60 m^2/ha);
2. 70% RBA-HF — 70% residual basal area (approximately 42 m^2/ha), with trees felled by hand and forwarded using a small rubber-tired line skidder (John Deere 440);
3. 70% RBA-FB — 70% residual basal area, with trees cut with a tracked John Deere 639 feller-buncher fitted with a Lokomo cone saw, and forwarded using a larger rubber-tired grapple skidder (John Deere 640);
4. 50% RBA-HF — 50% residual basal area (approximately 30 m^2/ha), using hand falling and a small line skidder; and
5. 50% RBA-FB — 50% residual basal area, using the feller-buncher and the large grapple skidder.

Skid trails were spaced approximately 20 m apart and were laid out prior to harvesting. The volume removed from the trails was not included in calculations to retain 70 and 50% of the basal area. The buffers around each treatment unit were cut to 70% residual basal area using a feller-buncher and grapple skidder. Harvesting started at Beedy Creek in July 1991, and was completed at the UBC Forest site in September 1991. Trees were not marked prior to cutting, but the logging contractors were shown how to use cruising prisms to select stems to meet the residual basal area targets.

All cutting was done by "thinning from below." The light removal treatment, leaving 70% residual basal area, was considered a "preparatory cut" (Smith 1986; Matthews 1989; Nyland 1996), removing suppressed and intermediate trees from the lower crown classes. The heavy removal treatment, leaving 50% residual basal area, was considered a "seed cut," with some codominant trees in the upper and intermediate crown classes removed along with the suppressed and intermediate trees. In all treatments, healthy and well-formed trees were retained with regular spacing where possible, with preference for Douglas-fir over lodgepole pine over spruce; any hardwoods were removed. Topping and limbing were done on site when falling was done by hand, or at the landing when done by feller-buncher. Where clusters of advance regeneration (especially larger seedlings and saplings) were evident, efforts were made to leave them undamaged.

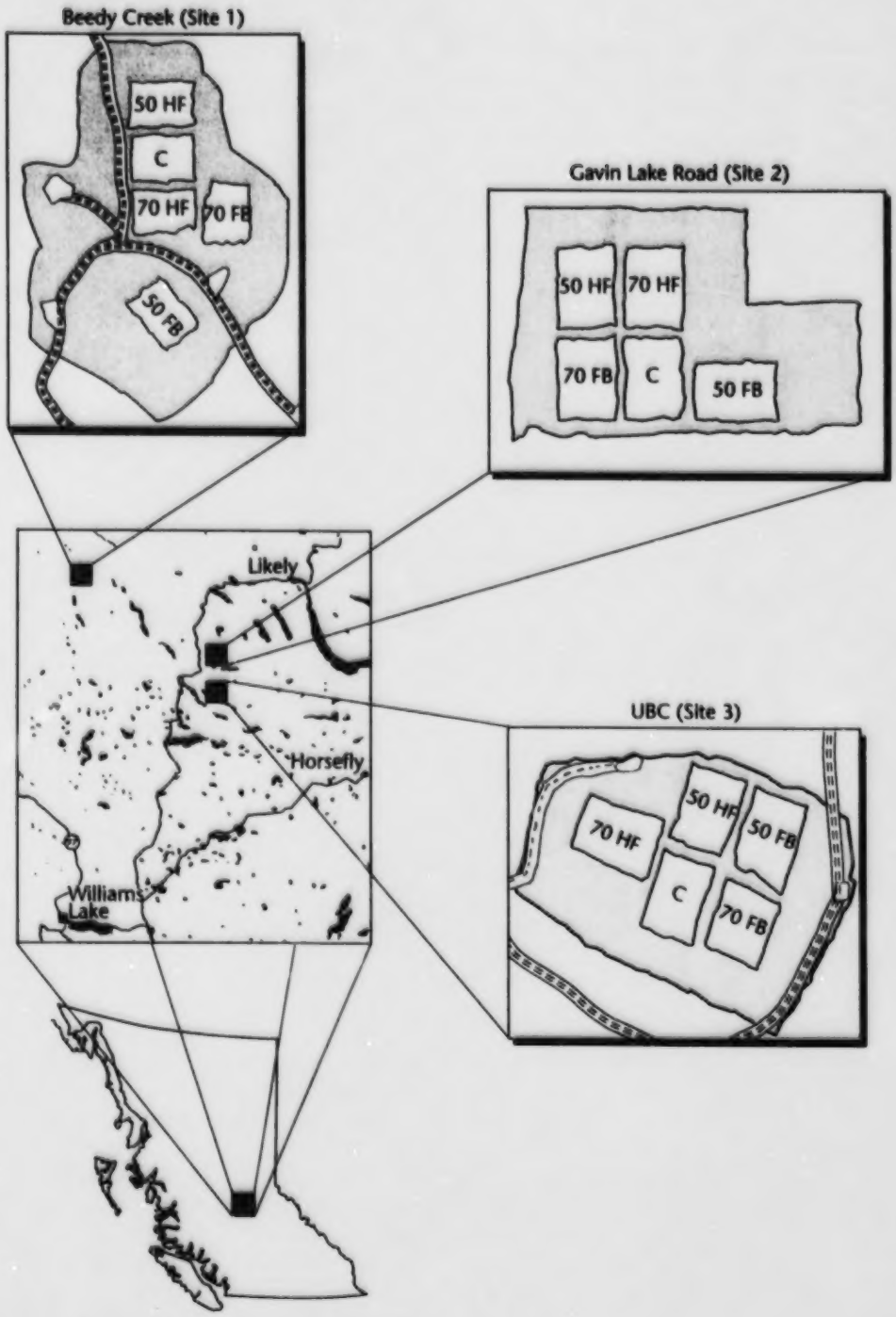

FIGURE 1 *Location of study sites and treatment units at each site.*

2.3 Stand Structure Assessment

Within each treatment unit, 15 permanent cruise plots were established in order to determine pre- and post-harvest stand structure. Three rows of five plots each were established on a 20 × 20 m grid. One year prior to harvest (1990), a variable radius plot (basal area factor 4) was established at each plot centre, and data were collected following procedures specified in the Ministry of Forests Cruising Manual. Stems were measured down to a minimum of 7.5 cm diameter at breast height (dbh).

These plots were reassessed immediately following harvesting (1991), and again after windthrown trees and those infested by (or at risk from) bark beetles had been salvage logged (1994). Stem measurements were tallied in 10-cm dbh classes, and were also converted to estimates of basal area (m^2/ha) for each species in each treatment unit. These calculations allow determination of the basal area actually removed in harvesting operations, and document the residual basal area and stand structure and how they vary over time and among treatment units.

2.4 Microclimate Monitoring

Environmental sensors and dataloggers were installed in the control, 70% RBA-FB, and 50% RBA-FB treatment units at the Beedy Creek site, and in a nearby clearcut (0% RBA) to provide representative descriptions of the microclimate under each stand treatment from 1991 to 1995. Stevenson screens were installed at 1.2 m above the ground in all four treatments to obtain a set of standard meteorological air temperature and relative humidity measurements. Quantum radiation sensors were installed on top of these screens in the clearcut and control treatment units. Precipitation, wind speed, and wind direction were monitored only in the clearcut.

Campbell Scientific CR10 dataloggers and AM-416 multiplexers were used for environmental data collection in all four treatments, except in the clearcut where no multiplexer was employed. Three replicate profiles of temperature and soil moisture sensors were established to better sample the variability inherent in forest understories, and to reduce the risk of missing data due to sensor malfunction. Air temperature for each profile was measured at 15 cm above the ground using a thermistor temperature probe. Soil temperatures were monitored using thermistor probes installed at 1, 5, 15, 25, and 50 cm beneath the forest floor / mineral soil interface. A single profile was sampled in the clearcut, with no 50 cm soil depth represented. Soil water potential was monitored with gypsum blocks at the 5 and 15 cm depths in each soil profile in each treatment. Sensors were read every minute, with daily mean, maximum, and minimum values saved to memory. Data summarization emphasized monthly means and integrals summed over the growing season. Heat sums were determined for air temperatures at 15 cm, based on a 5°C threshold, to calculate growing degree-days from May 15 to September 23 of each year. An analogous water stress integral (Myers 1988) was determined for soil water potential, using -0.3 bars as a threshold, to calculate bar-days of cumulative moisture stress over a similar interval. Hard frost events (daily minimum air temperature <-2°C) at 15 cm were also counted during each year's growing season.

Because of the variability in canopy conditions, an effort was made to more precisely document the relative irradiance experienced on the forest floor under each removal treatment. Hemispherical photographs of the canopy were taken (under overcast conditions) during the summer of 1995 at the surface of each of the 12 germination plots (described in Section 2.8) situated in all control units in the 70% RBA-FB and 50% RBA-FB treatment

units. These photographs were digitally scanned and analyzed using a solar radiation model (GLI/C Version 2.0; Canham 1988) to describe the light regime experienced during the growing season (specified as April 15 to September 15) at each spot. Results are given for global irradiance (the sum of beam plus diffuse components) relative to that of a completely open sky.

2.5 Seed Rain

Ten seed traps per 1.4 ha treatment unit were laid out in the control, 70% RBA-FB, and 50% RBA-FB treatments in August 1992. Traps consisted of a 0.61 × 0.61 m wooden frame (0.37 m^2 area) holding a nylon fabric collection bag, covered with a removable lid with 0.8 cm wire screening stapled to another wooden frame, designed to exclude rodents (Leadem et al. 1997, p. 77). These traps were situated at 10 points randomly selected from 48 points on a 15 m grid surveyed in each treatment unit.

Interior Douglas-fir generally disperses seeds from August through September, while lodgepole pine and hybrid white spruce shed seeds from September to October (Eremko et al. 1989). Though most interior populations of lodgepole pine usually bear serotinous cones, some cones in undisturbed stands typically open under normal temperatures, and the number that open can increase after logging disturbance (Eremko et al. 1989). Seed traps were inspected in October from 1992 to 1997, and again in April or May from 1994 to 1998, in order to more completely sample seed production from the previous year. Organic material found in each trap was taken back to the lab, where seeds were separated from plant litter, identified to species, counted, and assessed for viability. Seeds were considered viable if they had mature, intact embryos and complete, firm megagametophytes, as determined when cutting the seed open with a razor blade (Leadem 1984). Douglas-fir seeds were assessed for viability at each sampling interval, while the viability of hybrid white spruce seeds was determined only in 1992 and 1993. Where viability was not assessed using the cutting test, seeds were rated as mature (full sized, plump and firm, dark coloured) or immature. The numbers of viable or mature seeds of each species per trap were then combined for fall and spring sample periods, and then multiplied by 27 027 (= 10 000 m^2 per ha or 0.37 m^2 per trap) to give seed rain density at each sample point in terms of seeds·ha^{-1}·yr^{-1}. Seed samples collected before 1994 did not distinguish between hybrid white spruce and lodgepole pine, with all reported as "spruce."

2.6 Seed Predation

Ten seed predation quadrats were installed in the vicinity of seedfall traps (i.e., at 10 random locations in each 1.4 ha treatment unit). Seeds of interior Douglas-fir collected nearby were used, after having been processed (dewinged) and stored at the Ministry of Forests Tree Seed Centre. Only filled mature seeds were used. Ten individual seeds were placed on the surface of the forest floor in each 0.61 × 0.61 m quadrat. The positions of individual seeds were marked with plain wooden toothpicks stuck into the forest floor approximately 0.5 cm from each seed. No barriers to seed movement or rodent activity were installed.

Seeds were positioned in September 1992, May 1995, and May 1996. They were then inspected at approximately 3-week intervals until snow persisted. Monitoring of the 1992 seeds or their replacements likewise continued from May until September in 1993. These dewinged Douglas-fir seeds were exposed to seed predators over a single 3-week period in the fall of 1992, over seven 2- to 4-week periods during the 1993 growing season, five periods during 1995, six periods during 1996, and over the 1992/93 winter period (approximately

200 days). Seed loss per monitoring period was divided by the number of days in that respective period, and expressed in percent loss per day, because the length of these intervals varied.

During each monitoring episode, every effort was made to re-locate individual seeds, with their fate recorded as "intact" (undisturbed or germinated), "missing" (not found, presumed eaten), or, in 1995 and 1996, "eaten" (confirmed predation, with seed hulls indicative of consumption by small mammals). Remains of eaten seeds were removed at each sampling session and replaced with whole seeds. Statistical analysis of seed predation was conducted using the sum of "missing" and "eaten" values, though some missing seeds may have been washed into the duff and may still germinate. Preliminary seed predation levels, plus small mammal population estimates for these shelterwood treatments, are reported elsewhere (von Trebra 1994; von Trebra et al. 1998).

2.7 Seedbed Distribution

One year prior to harvesting, measurements of duff (forest floor) thickness were taken at ten random points in each of ten regeneration survey plots (described in Section 2.9) in each treatment unit. These measurements served primarily to determine the similarity of initial conditions among locations and treatment units, and were not repeated in subsequent years.

Post-harvesting seedbed assessments concentrated on the percent surface cover of different substrate categories. The relative abundance of four substrate (seedbed) categories was estimated in each of five regeneration plots assessed in each treatment unit in 1991, soon after harvesting. Seedbed categories were the same as those used in recording the substrate of naturally regenerated seedlings (Section 2.9), namely, undisturbed duff or moss, disturbed duff or moss, rotting wood, and mineral soil. The abundance of these four seedbed categories in each 3.99 m radius (50 m^2) plot was visually estimated using five broad cover classes: 0 = 0% cover; 1 = 1–10% cover; 2 = 11–30% cover; 3 = 31–50% cover; and 4 = >50% cover.

A more intensive and detailed sampling effort was conducted in the fall of 1993. A 15 × 15 m sampling grid served as the framework for sampling the surface cover of different ground covers in the control, 70% RBA-FB, and 50% RBA-FB treatment units. The 48-point sample grid (six transects of eight points each) was situated at least 7.5 m from any treatment unit boundary. A randomly oriented metre stick was set on the ground at each grid point, and the length (in cm) of different materials intercepted by the metre stick was recorded according to 19 detailed categories. These categories were subsequently grouped as live moss, forest floor, mineral soil, rotting wood, and other (unsuitable) seedbeds. Surface cover at each sampling point always summed to 100% cover.

2.8 Seed Germination and Germinant Survival

Germination on different seedbeds under a range of canopy conditions was investigated as part of a larger project evaluating germination in the Interior Douglas-fir and Coastal Western Hemlock biogeoclimatic zones, as well as at these Sub-Boreal Spruce zone sites (Burton 1997). Plots measuring 60 × 30 cm were established to test the germination of several conifer species on each of four types of seedbed under each of four densities of residual canopy cover. Twelve of these germination plots (three for each seedbed type) were set up in each treatment unit logged by feller-buncher, in the controls and in nearby clearcuts, with plots evenly distributed among open (gap) microsites, closed (subcanopy) microsites, and microsites within dense clusters of large

advance regeneration. The standardized seedbed treatments included mineral soil, forest floor, rotting wood, and mats of living tericolous moss. Local mineral soils consisted primarily of sandy loam. Rotting wood was collected from the forest floor and included only friable material, with no chunks larger than 1 cm^3. Forest floor materials consisted primarily of mor or moder humus, though some less-decomposed litter (primarily conifer leaves) was inadvertently included too. These materials were always well mixed before being spread in germination plots. Moss mats consisted mostly of *Brachythecium* spp. and some *Pleurozium schreberi*.

Controlled substrates were spread in level spots with the existing forest floor first excavated from the site. Plot installation was designed to create a uniform seedbed with good hydraulic contact with the underlying mineral soil, though some barriers were required to exclude rodent seed predators. Each plot was enclosed by wire screening (hardware cloth) with a 0.8 cm mesh size. To hold the screening in place while facilitating its repeated removal and replacement, it was crimped around the frame of a plastic greenhouse flat from which the bottom had been cut out. When placed on the substrate plot and backfilled, this screen-covered tray presented a substrate surface flush with the forest floor and with rodent-excluding sides extending 6.5 cm down. Each plot was divided into eight subplots, with two subplots sown to each tree species in each plot. These methods are now recommended for widespread use, and are illustrated in Leadem et al. (1997, p. 124).

Fifty seeds per subplot were scattered on the surface of the seedbed materials in the autumns of 1993, 1994, and 1995. The seeds used were from commercial seed lots registered with the Ministry of Forests Seed Centre, donated by the B.C. Forest Service and local industry cooperators. All seeds had been dewinged, sorted, and stored for 1–14 years prior to use. Seed lots of each species were selected to represent provenances from spots as close as possible to the study area, preferably with high germination capacity (based on Seed Centre assays). Dry, unstratified seeds were counted out by hand, excluding any seeds that were obviously empty or misshapen. Seeds were sown in September or October of 1993, 1994, and 1995, allowing them to stratify naturally in the field. Prior to seeding, all previously installed seedbed material and any seeds or seedlings therein were first removed, and fresh substrate was put in place. Fifty seeds were scattered into each subplot, making sure that they were generally well spread, not touching each other, and not too close to the edges. After sowing, the lid (screened top) was replaced and backfilled to exclude rodents and to be flush with the ground surface.

Douglas-fir, hybrid white spruce, and lodgepole pine seeds were tested in all 3 years, while subalpine fir was also tested in the last 2 years. Germination plots were established and re-used each year in control treatment units, and in the 70% RBA-FB and 50% RBA-FB treatment units. Test plots were also established in nearby clearcut blocks or other large clearings, but only in 1995 (for monitoring in the 1996 growing season).

Monitoring followed both germination and survival of new germinants at approximately monthly intervals. New germinants were tallied and marked each month from May to September in 1994, 1995, and 1996, and the survival of previously marked cohorts was tabulated at the same time. All new seedlings (usually with full cotyledons, but counted if the emerging radicle was more than twice the length of the seed) in each compartment were first recorded. If more than 10 new seedlings were present in a subplot, then all but 10 well-spaced seedlings were removed. These seedlings (10 or fewer in

number) were then collared with hoops of coloured wire, with a different colour signifying each month of emergence. Previously tagged seedlings were counted, with any mortality and their tags removed. No effort was made to prevent natural seed rain onto the germination plots. However, levels of seed rain during this time period were generally so low (averaging less than one seed per 180 cm^2 subplot; see Section 3.3) that no adjustment was needed.

2.9 Natural Regeneration Density

Within each 1.4 ha treatment unit, 15 permanent survey points were established on a 20 × 20 m grid for monitoring the density, composition, and substrate of natural regeneration (all trees <7.5 cm dbh that were not planted). Sample plot centres were permanently marked with labelled cedar stakes. These plots were assessed 1 year prior to harvesting (autumn 1990), immediately after harvesting ("Year 0," autumn 1991), and again in 1993 ("Year 2"), 1994 ("Year 3"), and 1996 ("Year 5"). It is planned that these subplots will be relocated and sampled again in the year 2000, prior to the seed cut for the 70% RBA treatments, and in 2001 after that harvesting entry.

Sampling methods were refined as the monitoring program progressed. In 1990, 1991, and 1993, all regeneration was evaluated in a 3.99 m radius (50 m^2) circular plot at each sampling point. Sampling in 1994 and 1996 was more efficient, utilizing a set of three sizes of nested plots for different sizes of young trees (Table 1). These young trees were tallied in three separate size classes in 1990, 1991, and 1993, with an additional "germinant" class added in 1994 and 1996 (Table 1). It can be assumed that germinants and small seedlings had emerged within the previous year or two, while all medium (and smaller) seedlings detected in 1996 were probably initiated since harvesting

TABLE 1 *Sampling details and size class definitions used in regeneration sampling. Regeneration was always recorded by species.*

Year	Plots per trt. unit (number)	Plot area (m^2)	Regeneration size class criteria: Germinants (age)	Small (cm tall)	Medium (cm tall)	Large (cm tall)	Poles (cm ht–cm dbh)	Density recorded (how?)	Regeneration substrate (recorded?)
Pre-harvesting:									
1990	10	50		≤5.0		5.1–100	101–7.5 dbh	six classes*	no
1990	5	50		≤5.0		5.1–100	101–7.5 dbh	six classes	yes
Post-harvesting:									
1991	10	50		≤5.0		5.1–100	101–7.5 dbh	six classes	no
1991	5	50		≤5.0		5.1–100	101–7.5 dbh	six classes	yes
1993	15	50		≤5.0		5.1–100	101–7.5 dbh	counted	yes
1994	15	1	1–2 yr old	≤10.0†				counted	no
1994	15	10			10.1–30.0	30.1–100		counted	no
1994	15	50					101–7.5 dbh	counted	no
1996	15	1	1–2 yr old	≤10.0†				counted	no
1996	15	10			10.1–30.0	30.1–100		counted	no
1996	15	50					101–7.5 dbh	counted	no

* Density classes as follows: 0 = 0 stems per plot; 1 = one to three stems (200–600 sph); 2 = four to seven stems (800–1400 sph); 3 = eight to 19 stems (1600–3800 sph); 4 = 20 to 39 stems (4000–7800 sph); and 5 = 40+ stems per 50 m^2 plot (8000+ sph).

† Seedlings >2 years old.

in 1991. Observations made in 1990 and 1991 recorded only the number of seedlings per plot according to six density classes (see footnote to Table 1), but data collected after 1991 represent precise counts of seedlings by species.

Regeneration was recorded by four substrate categories (undisturbed duff/moss, disturbed duff/moss, rotting wood, or mineral soil) in five plots per treatment unit in 1990 and 1991, and in all 15 plots in 1993, but not at all in 1994 or 1996. Table 1 summarizes the sampling details and size class definitions associated with each year of monitoring. Unfortunately, only pole densities are precisely comparable across all 5 years of observations.

2.10 Growth of Natural Regeneration

A retrospective analysis of stem growth in naturally established seedlings was conducted in August 1994. Within each of the 50 m^2 permanent regeneration monitoring plots in each treatment unit, the four seedlings 25–100 cm in height closest to the plot centre (regardless of species) were selected for measurement. A fifth tree was selected outside of some of the permanent plots for destructive sampling to determine tree ages (for three to six trees per treatment unit). Growth rings were counted under a dissecting microscope. Most trees were Douglas-fir but a small component consisted of hybrid white spruce and subalpine fir. Each seedling was measured for basal diameter and height to the base of its apical bud. In addition, heights for the previous 4 years (1993, 1992, 1991, and 1990) were estimated from the points where whorls of branches emerged from the main stem. Because the amount of extension growth often showed an apparent relationship to the size of seedling, the primary response of interest was relative height growth, defined as measured height in 1994 minus estimated height for 1990, all divided by the 1990 height.

2.11 Statistical Analysis

The overall experiment and its monitoring program follow a randomized block design with subsampling. Results have been summarized and interpreted primarily by treatment, with the three locations serving as statistical blocks or true replicates; individual plot observations were considered subsamples. Unless otherwise indicated, all means and standard errors of the mean (SEM) presented in this report refer to the average and SEM of overall treatment unit means, not of individual subsamples (i.e., usually n=3).

Data from the 1990 and 1991 regeneration surveys were summarized according to the frequency of subplots in each of the density classes used in tallying seedlings, with separate compilations made for each year, tree species, and size class. Contingency table analysis (SAS procedure CATMOD; SAS Institute 1988a) based on a log-linear model using maximum likelihood estimation was employed to test for treatment effects, location effects, and their interaction. Chi-square values were calculated for treatment and location effects in terms of their interaction with the regeneration density classes. Separate runs of SAS procedure FREQ (SAS Institute 1988b), on treatment × density class and location × density class contingency tables, were used to calculate each cell's contribution to the total chi-square statistic, allowing us to draw conclusions regarding which treatments or locations were significantly higher or lower than others.

In order to facilitate some descriptive comparison of seedling densities among years, density classes recorded in 1990 and 1991 were also converted to estimated seedling densities, so that seedling density could be assessed as a continuous response variable in all years. Absolute seedling densities in 1990 and 1991 were estimated using the midpoint for each density class, with the

arbitrary "midpoint" of 11 460 stems/ha chosen for the highest density class (because it was the average of all species and size class combination means for 1993 plots having more than 40 stems per 50 m^2 plot). The following values were used for these estimates: density Class 0 is 0 stems/ha (sph); Class 1 is assumed to represent 400 sph; Class 2 is 1100 sph; Class 3 is 2700 sph; Class 4 is 5900 sph; and Class 5 is 11 460 sph.

Counts of seed rain density (1992–1998) and seedlings (1993, 1994, and 1996) per plot were converted to densities per ha prior to further summarization and analysis. Most response variables (i.e., seed rain density, percent cover of different substrates, percent germination, percent survival of germinants, and estimated stem densities) were summarized in terms of the mean and standard error under each treatment, followed by an analysis of variance for treatment effects. Because seed and seedling densities often spanned three or more orders of magnitude among treatments (and especially among years), observations were first log-transformed before being tested by analysis of variance. The procedure GLM was used for the analysis of variance (SAS Institute 1988a) in order to make planned contrasts among specific treatments. These planned contrasts evaluated both 70% RBA treatments (i.e., those logged by hand-falling and those logged by feller-buncher) in comparison with both 50% RBA treatments, and compared both hand-falling treatments (70% RBA and 50% RBA) with both feller-buncher treatments. The general analysis of variance model (e.g., for regeneration densities) employed was as follows:

Source of variation	Degrees of freedom	Error term
Location, L = 3	(L-1) = 2	—
Treatment, T = 5	(T-1) = 4	Location × treatment
Location × treatment	(L-1)(T-1) = 8	—
Plots, P=15	LT(P-1) = 210	—
Total	LTP-1 = 224	

Note that the location × treatment interaction term was used as the error term in calculating the F statistic for treatment effects. If the treatment effect was significant at the $p = 0.05$ level, then Scheffé's multiple comparison test was used to determine which treatments were significantly different from each other. Again, the location × treatment interaction term was specified as the appropriate error term, and $p = 0.05$ was used as the cutoff for interpreting significance. It is reasonable to relax the $p = 0.05$ significance level for an operational field trial of this sort, so some interpretations are drawn from results significant at the $p = 0.10$ level. All responses expressed as a percentage (e.g., seeds lost to rodents, or the cover of mineral soil seedbeds) were first arc-sine square-root transformed before being tested by analysis of variance.

We have also portrayed our best estimates of seedfall and regeneration densities as they have changed from year to year. Stem densities in 1990 and 1991 were estimated using density class midpoints and summed for all size classes, and then plotted (by species and treatment) along with densities from 1993, 1994, and 1996 to show trends over time. These combined data were also used to test for overall treatment effects across all years, in which variability due to year and year × treatment was accounted for before testing for treatment effects, with treatment nested within location used as the error term. No attempt was made to test for significant differences among species in any analyses reported here. Some tests were conducted to determine if

species differed in their ability to establish on different substrates, and are reported elsewhere (Leadem et al. 1997, pp. 141–3).

2.12 Synthesis

A few correlations were explored between various components of natural regeneration and their environment. For example, seed rain density in different treatment units was related to each unit's basal area, and to seedling densities observed the next year. Likewise, germination and survival rates were correlated with microsite measurements of relative irradiance, heat sums, and moisture stress, though such measurements were available for only six of nine cases. We also used stepwise multiple regression (SAS procedure REG, with the maximum r^2 improvement option; SAS Institute 1988a) to determine the three variables most predictive of the observed densities of new Douglas-fir seedlings. Data collected from three treatment units at the three locations over each of 1993, 1994, and 1996 limited the sample size for most of these analyses to n=27.

Many of the relationships among the variables explored using correlation and regression analysis actually function in a sequential manner. Observed densities of conifer germinants at the end of their first year should be equal to the seedfall density experienced in the previous year, less losses to seed predation, times the relative abundance of each seedbed category and the germination rates and germinant survival rates observed for each seedbed, as summed for all seedbed types. Each of these phenomena is influenced by the micro-environmental factors explored in the correlation analysis above, which are ultimately determined by stochastic differences in weather, as mediated by the residual basal area and canopy cover. A simple spreadsheet model was devised to synthesize the various influences on the density of natural regeneration as studied in this experiment. This exercise was conducted only for Douglas-fir regeneration, because this is the only species for which we had seed predation data, and it is the crop species for which the silvicultural prescription was developed.

Figure 2 portrays a conceptual model of the interaction of factors affecting the density of new seedlings in partially cut stands, indicating those components for which we have data. The model was exercised in three treatment units (those for which we had seed rain, seed predation, and germination results) at each location in 1993, 1994, and 1996, the years for which we have accurate seedling densities. In each unit, the expected density of new regeneration, r, at the end of each year, t, can be described as:

$$r_t = f_{t-1} \cdot (1-p) \cdot \sum_{s=1}^{4} c_s \cdot g_s \cdot v_s$$

where f is seedfall density, p is cumulative seed predation between seedfall and germination, s denotes each of four different seedbeds for which we have obtained percent cover values, c, and observations on percent germination, g, and percent germinant survival, v. Cumulative seed predation, p, was calculated as $1-(1-p_f)(1-p_w)$ where p_f and p_w represent the average percent seed loss observed over fall (September and October) and winter (November to April) monitoring periods, respectively. Seed predation values during the winter were observed only for the 1992/93 season, so those rates were assumed to hold in all years. All values were specific to the different RBA treatments implemented at each of the three locations.

Predicted densities of seedlings were compared to densities of small seedlings (<5 cm tall) or germinants observed in that same year using chi-square

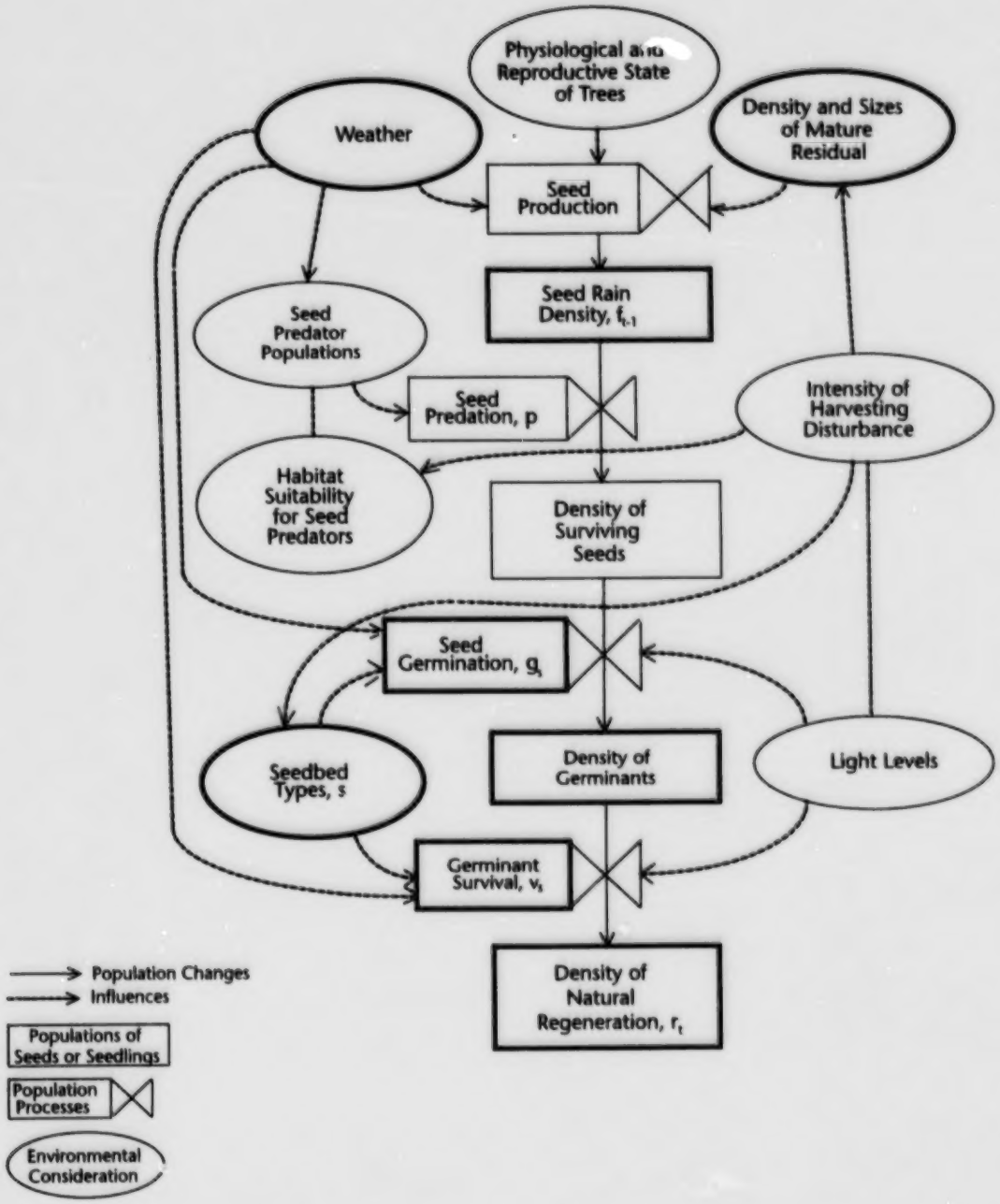

FIGURE 2 *Conceptual model of natural regeneration in partially cut stands. Data were collected on the components outlined in* **bold**. *Abbreviations for different model components are used in the formula given in Section 2.12 and in Table A3.2.*

and correlation analysis. Since estimation of model variables and of seedling density were both subject to sampling error, two methods were used to evaluate how well predicted densities agreed with observed densities. First, mean estimates for seedfall density, seedbed cover, germination, and germinant survival were used in the model, and were compared with the 90% confidence interval for observed regeneration densities. Secondly, those four variables were set to their lower 90% confidence limits, and then to their upper 90% confidence limits, to generate a range of predicted densities for comparison with mean observed seedling densities. Seed predation estimates were not varied because they had been derived as single values for each treatment unit and hence have no confidence limits associated with their estimation. The degree to which predicted and observed seedling densities agree is an indication of the extent to which we have adequately identified the processes responsible for successful natural regeneration.

3 RESULTS

3.1 Stand Structure after Harvest

Prior to harvest, treatment units had basal areas ranging from 52.0 to 69.1 m^2/ha, with an overall mean of 61.2 m^2/ha (Table 2). Analysis of variance revealed no significant difference in pre-harvest basal area among the units scheduled to receive different treatments ($F_{4,10} = 0.70$, $p = 0.61$). All control units and pre-harvest stands had a similar stand structure, with an average stem diameter of 28 cm dbh and a fairly uniform density of trees spanning the 15–40 cm dbh size classes (Figure 3a).

Harvesting treatments came very close to meeting their objectives for residual basal area, though hand-falling generally left more basal area than the feller-buncher (Table 2). Both of the 50% residual basal area treatments were shy of their mark, leaving an average of 56.1% of the original basal area in the 50% RBA-HF units and 55.6% of the original basal area in the 50% RBA-FB units. Furthermore, the variability in the 50% RBA-HF treatments was such that their post-harvest basal area was not statistically distinguishable from that in any of the other partially cut treatments. Salvage operations in 1992 and 1993, however, left the three residual basal area treatments statistically distinct in 1994 ($F_{4,10} = 62.00$, $p = 0.0001$), with no significant differences attributable to the method of harvest. Harvesting removed most of the smaller trees, many of the pine, and almost all of the hardwoods, while leaving almost all of the large (>42.5 cm dbh) Douglas-fir trees (Figures 3b and 3c). This shift in stand structure to a higher proportion of large trees is confirmed by the fact that post-harvest dbh averaged 34 cm in the 70% RBA units and 36 cm in the 50% RBA units.

The proportion of merchantable timber volume left in each treatment unit was always slightly greater than the proportion of basal area left standing (Table 2). Across all 70% RBA treatment units, residual volume in 1994 was an average of 76.5% of pre-harvest volumes, compared to 70.6% of pre-harvest basal area. Similarly, the final residual volume in the 50% RBA units averaged 58.8%, compared to 52.6% of pre-harvest basal area.

Repeated stand sampling has documented continued growth by the overstory trees. All control units showed a slight increase in basal area from 1990 to 1991; this did not continue to 1994 because of salvage operations. Despite the salvage of windthrown and beetle-infested trees, most treatment units showed an increase in merchantable volume from 1991 to 1994 (Table 2).

TABLE 2 *Basal area and volume of standing trees* prior to harvest, immediately after harvest, and after salvage operations had removed windthrown trees and those subject to bark beetle infestation*

Location	Treatment unit	Residual basal area (m^2/ha)			Residual merchantable volume† (m^3/ha)		
		1990	1991	1994	1990	1991	1994
		(pre-harv.)	(post-harv.)	(post-salvage)	(pre-harv.)	(post-harv.)	(post-salvage)
Beedy Ck.	100% RBA	69.1	69.2	60.0	676.2	666.4	619.1
	70% RBA-HF	62.4	45.4	45.1	605.0	437.1	469.1
	70% RBA-FB	61.1	46.2	45.6	621.2	494.6	511.3
	50% RBA-HF	58.9	36.8	33.6	614.0	403.9	376.3
	50% RBA-FB	53.3	31.8	30.9	553.0	356.4	348.8
	Mean:	61.0			613.9		
Gavin Rd.	100% RBA	64.3	64.6	63.7	647.7	642.7	685.3
	70% RBA-HF	65.1	43.0	41.3	654.4	431.8	450.0
	70% RBA-FB	63.5	42.7	42.7	652.8	446.6	473.7
	50% RBA-HF	68.3	35.6	33.6	692.9	364.0	368.8
	50% RBA-FB	57.9	32.2	28.5	600.3	329.1	310.7
	Mean:	63.8			649.6		
UBC	100% RBA	60.0	60.3	59.7	555.6	566.0	603.6
	70% RBA-HF	52.0	42.1	40.8	498.5	413.0	420.0
	70% RBA-FB	54.7	37.9	36.8	528.2	369.0	386.7
	50% RBA-HF	62.9	33.7	32.5	569.7	320.0	332.8
	50% RBA-FB	64.3	33.1	32.3	490.0	293.0	319.8
	Mean:	58.8			528.4		
		(=100%)	(mean %)	(mean %)	(=100%)	(mean %)	(mean %)
Means, all sites	100% RBA	64.5	100.4	95.1	626.5	99.9	102.0
	70% RBA-HF	59.8	73.3	71.4	586.0	73.7	76.9
	70% RBA-FB	59.8	70.7	69.7	600.7	72.6	76.0
	50% RBA-HF	63.4	56.1	52.6	625.5	58.2	57.6
	50% RBA-FB	58.5	55.6	52.5	547.8	59.7	60.0
	Mean:	61.2			597.3		

* Live merchantable trees only, excluding all dead stems and all those <7.5 cm dbh.
† Stump height 30 cm, top diameter 4 cm.

3.2 Weather and Microclimate

Electronic monitoring of daily weather conditions in a standard Stevenson screen situated in a clearcut near the Beedy Creek site for five growing seasons allowed us to compile a partial climate diagram for the study area (Figure 4). Mean annual temperature was 4.6 °C, with mean daily maxima of 21.7 °C observed in July (the warmest month), and mean daily minima of -9.9 °C observed in February (the coldest month). Extreme temperatures of 32.4 °C and -30.0 °C were observed on July 24, 1994, and February 25, 1994, respectively, demonstrating the continental nature of the climate. The mean growing season interval between frosts (0 °C) was 114 days. Four months a year have mean monthly temperatures below 0 °C, while 5 months have means above 10 °C. On average, the highest levels of precipitation were experienced in November (mean of 44.3 mm) and August (mean of 43.8 mm). However, the water equivalent of precipitation that fell as snow could not be accurately determined using the available equipment, so winter precipitation is not shown in Figure 4 and we do not have an accurate estimate of mean

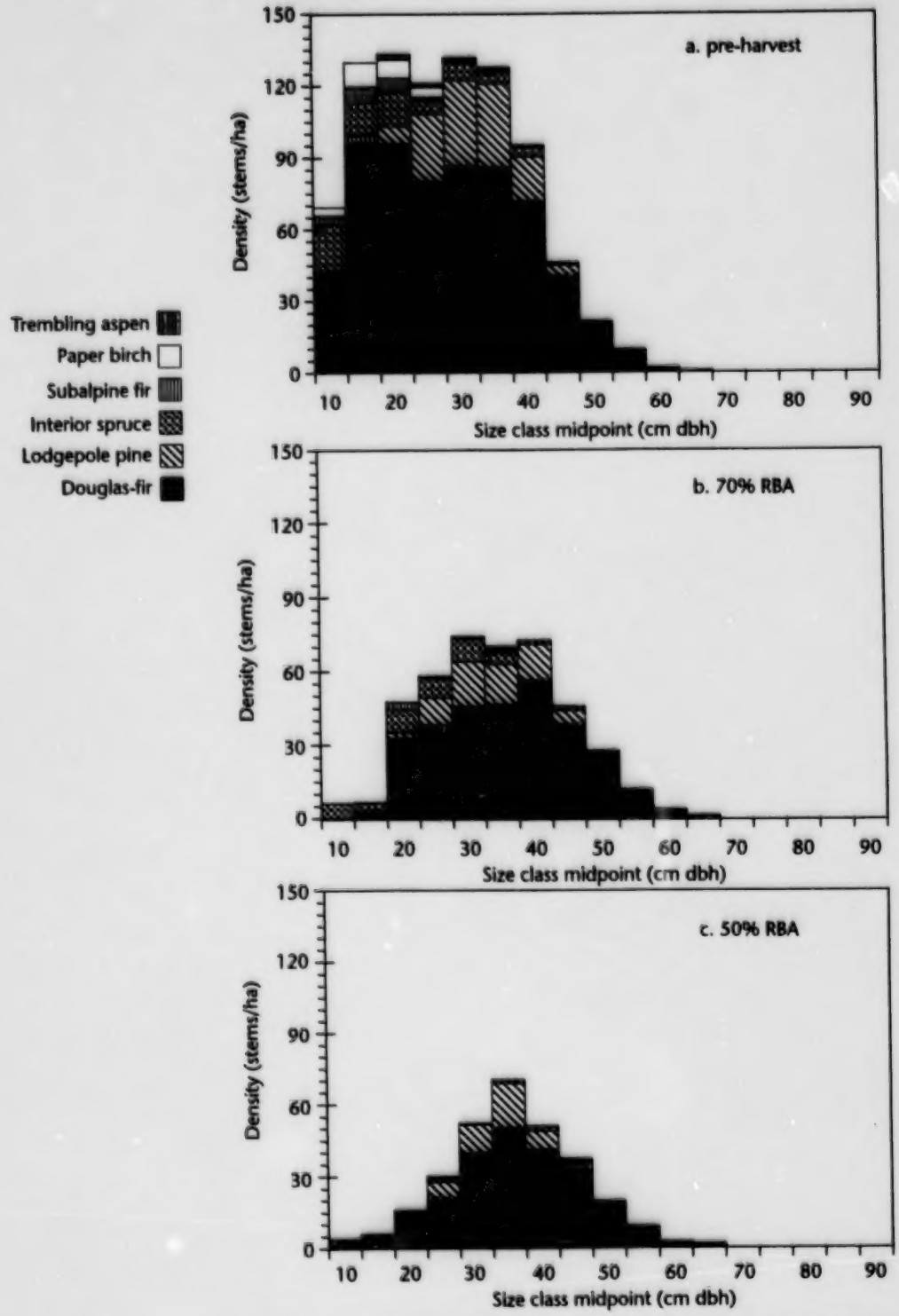

FIGURE 3 *Average stand structure of canopy trees (>7.5 cm dbh) at the three study sites, summarized for (a) pre-harvest conditions, (b) 70% residual basal area treatment units, and (c) 50% residual basal area treatment units.*

annual precipitation. The fact that the mean monthly precipitation line dips below the mean monthly temperature line when plotted on a scale of 1 °C = 2 mm precipitation (Figure 4) indicates a period of relative drought from May to July. The mean interval between detectable rainfall events from April through September averaged only 4.4 days, but each growing season experienced at least one interval of 12 or more days without precipitation; 1993 was particularly extreme, with no detectable rainfall from June 10 until August 21, a period of 72 days.

Year-to-year differences in local weather and treatment effects on microclimate are documented in Table 3. Measurements of photosynthetic photon flux density (PPFD) made at fixed locations over several years indicate that the understory of the control stand experienced only 6.7% of the photosynthetically active irradiance found in the clearcut. Using hemispherical photographs to sample 12 spots in the control unit at Beedy Creek, we found that relative irradiance there averaged 10.7% of full sunlight, or 13.6% of that sampled in the clearcut (which is less than 100% full sunlight because of stand edge effects and shading from shrubs and herbs). Across all three locations, relative irradiance measurements modelled from hemispherical photographs indicate that stand treatments did not result in a dramatic increase in subcanopy light levels: the 70% RBA-FB treatments removed an average of 30.3% of stand basal area or 27.4% of stand volume (Table 2), but produced light levels of only 13.4% relative irradiance (or 20.6% of that measured in clearcuts); similarly, the 50% RBA-FB treatments removed an average of 47.5% of the basal area or 40.0% of the volume (Table 2), but generated light levels of only 22.6% relative irradiance (34.8% of that measured in clearcuts).

Though dry, the 1993 growing season was not unusually warm. Mean air temperatures at 1.2 m were remarkably similar across treatments and among years. Nevertheless, heat sums above a threshold of 5 °C (measured 15 cm above the ground) accumulated in direct proportion to the degree of canopy opening (Table 3). The 70% RBA treatment resulted in a 2.2% mean increase in growing degree-days over that measured in uncut forest, while the 50% RBA treatment created a 6.7% increase, and 0% RBA (the clearcut) stimulated a 29.0% increase. Any degree of forest cover drastically reduced the incidence

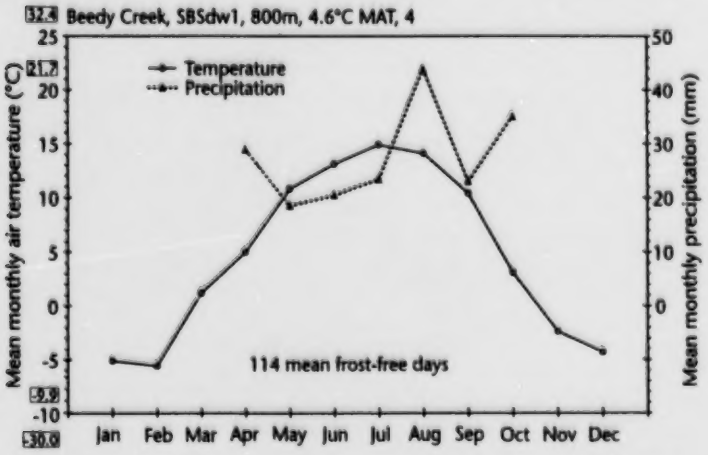

FIGURE 4 *Partial climate diagram derived for the Beedy Creek site. Winter precipitation and hence total annual precipitation are not accurately known.*

TABLE 3 *Mean growing season environmental conditions experienced under different stand treatments at the Beedy Creek site, 1991–1995*

Environmental attribute	Year	Stand treatment: 100% RBA (uncut)	70% RBA	50% RBA	0% RBA* (clearcut)
Relative irradiance (% full global irradiance, at 15 cm; modelled from hemispherical photographs, April 15–Sept. 15)					
Beedy Creek only:	1995	10.7	16.2	20.8	78.5
all three locations:	1995	6.5	13.4	22.6	64.9
Photosynthetic photon flux density at 1.5 m height (mean $\mu E \cdot m^{-2} \cdot s^{-1}$) (May 27–Sept. 20)	1991	(23.1)	--	--	(362.1)
	1992	25.2	--	--	383.9
	1993	21.3	--	--	353.4
	1994	27.5	--	--	361.5
	1995	25.3	--	--	358.2
	Mean:	24.5			363.8
Air temperature (°C, daily means at 1.2 m) (May 15–Sept. 23)	1991	13.3	(10.6)†	(10.7)†	13.5
	1992	13.7	13.9	13.8	13.3
	1993	13.0	13.0	(9.3)†	12.7
	1994	13.8	13.9	13.2	13.7
	1995	12.3	13.1	12.4	12.9
	Mean:	13.22	13.48	13.13	13.22
Heat sums >5°C (degree-days at 15 cm) (May 15–Sept. 23)	1991	(1061)	--	--	(1396)
	1992	1155	1273	1170	1493
	1993	1016	1015	1067	1392
	1994	1116	1111	1252	1432
	1995	1039	1020	1127	1264
	Mean:	1081.5	1104.8	1154.0	1395.4
Hard frosts <-2°C (number at 15 cm) (May 15–Sept. 23)	1992	1	3	1	13
	1993	1	1	0	8
	1994	0	0	0	4
	1995	0	0	3	11
	Mean:	0.5	1.0	1.0	9.0
Precipitation (mm) (May 1–Sept. 23)	1992	--	--	--	169
	1993	--	--	--	71
	1994	--	--	--	85
	1995	--	--	--	273
	Mean:	--	--	--	149.5
Moisture stress integral, soil tension >0.3 bars at 5 cm depth (bar-days) (May 1–Sept. 20)	1992	1299	1426	1030	837
	1993	945	415	1314	488
	1994	985	590	1299	391
	1995	286	161	753	281
	Mean:	878.8	648.0	1099.0	499.3
Moisture stress integral, soil tension >0.3 bars at 15 cm depth (bar-days) (May 1–Sept. 20)	1992	294	1285	1022	992
	1993	114	281	1348	635
	1994	431	286	1544	549
	1995	58	56	1776	393
	Mean:	224.3	477.0	1422.5	642.3

* RBA = residual basal area.
† not used in calculating means.
( ) = incomplete or based on some estimated values.

of hard frosts during the growing season (defined as temperatures <-2 °C from May 15 to September 23): four to 13 (an average of nine) hard frosts were experienced in the clearcut every year, but only one to three occurred in uncut or partially cut treatment units (Table 3). We can therefore conclude that both shelterwood treatments have been largely successful in meeting one of their primary objectives, namely the avoidance of ground-level frosts during the growing season.

The prolonged drought in 1993 is evident as very low growing season precipitation (71 mm) that year (Table 3). In contrast, growing season precipitation in 1995 was 273 mm, almost four times greater. The 1993 drought was also expressed as a high moisture stress integral at 5 cm depths in the 50% RBA treatment, but was not evident in any other treatment units nor at the 15 cm depth (Table 3). The 50% RBA site experienced the greatest moisture stress (at both depths sampled) every year except 1992, when the 70% RBA treatment experienced more stress. Averaged over all 4 years of soil moisture sampling, there was more moisture stress at 5 cm than at 15 cm for the 100% RBA and 70% RBA treatments, but this trend was reversed for the 50% and 0% RBA treatments.

3.3 Seed Rain

Measurements of seed rain density referred to in this section denote viable seeds (as determined from cutting tests) or mature seeds only, unless otherwise indicated. Lodgepole pine and subalpine fir made relatively sparse contributions to the seed rain, always less than 93 000 mature seeds·ha^{-1}·yr^{-1} (lodgepole pine) or 71 000 seeds·ha^{-1}·yr^{-1} (subalpine fir) in all treatments (Table 4). Average Douglas-fir seedfall density ranged from less than 1000 viable seeds·ha^{-1}·yr^{-1} in 1997 to a peak of 1.92 million seeds·ha^{-1}·yr^{-1} in 1993. Hybrid white spruce seed production peaked at an average of 387 220 seeds·ha^{-1}·yr^{-1} in 1994, followed by a minimum of 17 348 seeds·ha^{-1}·yr^{-1} in 1995. Only Douglas-fir in 1995 showed a significant difference among treatments, with seed rain in the partially cut stands (averaging 614 640–730 030 seeds·ha^{-1}·yr^{-1}) being greater than in 100% RBA units (266 466 seeds·ha^{-1}·yr^{-1}). Contrasts between 50% RBA and 70% RBA were not significant at even the $p = 0.10$ level in any year.

Douglas-fir generated the greatest seed rain density in 1992, 1993, and 1995, while hybrid white spruce was more productive in 1994, 1996, and 1997 (Table 4), assuming that "mature seed" and "viable seed" determinations are more or less equivalent. Douglas-fir seed rain exceeded 43 000 seeds·ha^{-1}·yr^{-1} in all treatments in every year except 1997, peaking in 1993 with an average of 2 213 514 seeds·ha^{-1}·yr^{-1} in control plots (Figure 5). There was a secondary peak in 1995, though seedfall was then greatest in the 50% RBA treatment units.

Seedfall density of all species was highly variable within stands and among locations. The most pronounced differences were year to year, with Douglas-fir seed production in 1993 (1.92 million seeds/ha) being significantly greater than in all other years, and production in 1995 (540 000 seeds/ha) significantly greater than in all remaining years except 1994 (Figure 6). Based on the ratio of each main effect Type IV sums of squares to corrected total sums of squares calculated on log-transformed data, these year-to-year effects accounted for 88.5% of the overall variation in Douglas-fir seed rain, compared to a location effect of only 1.3% and a treatment effect of less than 0.3%. Note that the Beedy Creek stands failed to show the same secondary peak in seed production observed in 1995 at the Gavin Road and UBC sites (Figure 6).

TABLE 4 *Estimated densities of mature or viable* seeds (1000's, mean number/ha, ± S.E.†) summarized over all three locations from 1992 to 1997*

Year	Species‡	Overall mean	Treatment			ANOVA results	
			100% RBA	70% RBA	50% RBA	F	Prob.>F§
1992	spruce and pine*	2.1±0.9	1.8±1.8	2.7±1.6	1.8±1.8	0.00	1.00
	Douglas-fir*	80.5±27.0	58.6±30.3	73.0±12.8	109.9±83.4	0.72	0.54
1993	spruce and pine*	408.7±141.1	546.8±402.8	372.1±148.5	307.2±197.8	2.20	0.23
	Douglas-fir*	1924±279	2214±666	1757±442	1803±479	2.85	0.17
1994	hybrid white spruce	387.2±163.3	620.7±499.3	299.1±131.4	241.8±108.6	0.07	0.94
	Douglas-fir*	177.2±21.1	191.0±30.4	180.2±36.7	160.5±53.4	0.06	0.95
	lodgepole pine	69.5±13.1	92.8±33.1	73.0±16.9	42.6±5.7	3.47	0.13
1995	subalpine fir	0.6±0.4	1.9±1.0	0±0	0±0	3.88	0.12
	hybrid white spruce	17.3±3.2	17.4±9.4	14.8±5.0	19.9±2.2	0.33	0.74
	Douglas-fir*	537.0±124.2	266.5±96.0 b	614.6±215.0 a	730.0±267.5 a	21.93	**0.0070**
	lodgepole pine	23.7±5.4	22.9±8.4	28.9±9.7	19.4±12.8	0.61	0.59
1996	subalpine fir	28.0±22.7	70.3±68.9	2.0±1.0	11.7±9.1	0.42	0.68
	hybrid white spruce	107.6±24.4	151.4±67.5	97.1±8.7	74.3±30.6	0.88	0.48
	Douglas-fir*	46.8±9.1	49.5±18.9	47.3±15.4	43.5±19.9	0.54	0.62
	lodgepole pine	35.6±5.9	46.8±10.4	39.3±10.8	20.6±3.6	2.10	0.24
1997	subalpine fir	1.2±1.2	3.6±3.6	0±0	0±0	0.93	0.47
	hybrid white spruce	63.4±21.7	85.5±64.3	40.3±10.9	64.3±29.8	0.12	0.89
	Douglas-fir*	0.6±0.4	0.9±0.9	0±0	0.9±0.9	0.37	0.71
	lodgepole pine	32.2±4.0	34.4±9.3	37.0±5.0	25.2±6.3	3.02	0.16

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed seed densities followed by Scheffé's multiple comparison tests; means in the same line subtended by the same letter are not significantly different at the p = 0.05 level. **Bold** numbers indicate statistically significant results.

* Viable seeds of Douglas-fir (and spruce and pine in 1992 and 1993) as determined by cutting tests; all others denote visually mature seeds only.

† Means and standard errors are calculated from treatment unit means, not subsamples.

‡ Hybrid white spruce and lodgepole pine were not distinguished in 1992 and 1993, and subalpine fir was not recorded in 1992, 1993, or 1994.

§ If Prob.<0.05 then the treatment effect is significant at the 95% confidence level.

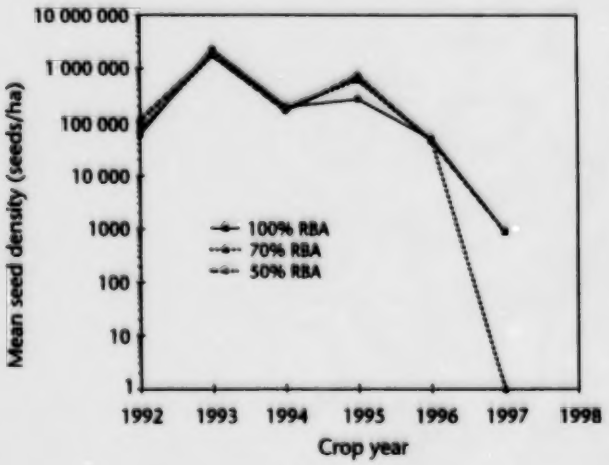

FIGURE 5 *Input of viable Douglas-fir seeds over time, for each of three canopy removal treatments, all three locations combined. (RBA = residual basal area.)*

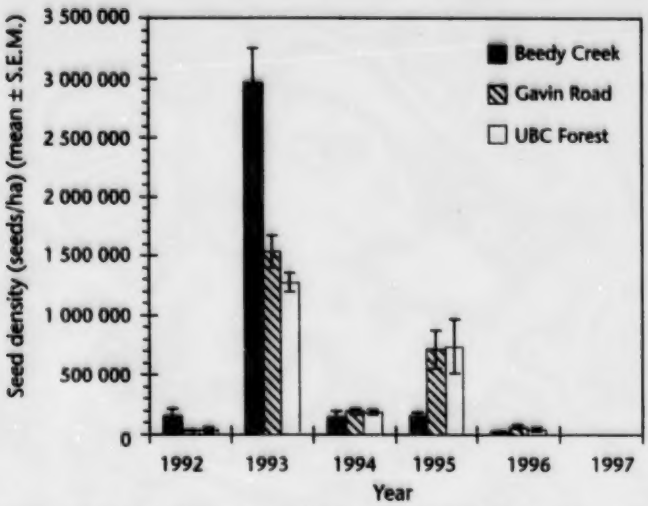

FIGURE 6 *Mean densities of viable Douglas-fir seeds at each location, all treatments combined.*

Douglas-fir seed production in individual treatment units showed no relationship to the basal area of canopy trees remaining in the unit, except in 1995. In that year, there was a marginally significant negative relationship between viable Douglas-fir seed rain density and stand basal area ($r = -0.60$, $p = 0.086$, $n = 9$). This negative relationship denotes greater seed production per residual tree under the partially cut treatments, though stand treatments had no effect in other years, including the important 1993 seed production year.

Data portrayed here denote only the mature, filled seeds considered viable. The proportion of all Douglas-fir seeds assessed as viable is a function of the overall size of seed crop in a manner that can be described by the following relationship: percent viable seeds = 49.2913 / (1 + 323751.7649 / total seeds per ha); $r^2 = 0.68$, $n = 54$. An even tighter relationship is obtained if the density of viable seeds is used as the independent variable: percent viable seeds = 90.0087 / (1 + 445051.3144 / viable seeds per ha); $r^2 = 0.89$, $n = 47$ (Figure 7).

3.4 Seed Predation

Seed predation on dewinged, filled Douglas-fir seeds was monitored over a total of 18 periods lasting 2–4 weeks each during the growing season, plus another interval assessed over the winter of 1992/93, representing 4 calendar years and 7 different months. When evaluated by expressing the ratio of individual factor Type IV sums of squares to the corrected total sum of squares in four separate single-factor analyses of variance, the variance attributable to yearly differences was 26.8%, to time of year 30.2%, and to location 3.6%, while the variance attributable to the removal treatments was only 1.3%.

Year-to-year differences in average levels of seed predation are summarized by stand treatment in Figure 8. Seed predation was determined to be significantly greater in 1996, followed by 1995 and then by 1993 ($F_{2,8} = 54.62$, $p = 0.0001$). There was also a significant effect attributable to the time of year. Across all treatments and years, seed predation in all earlier months was significantly greater than in October, and predation in winter (expressed on a per day basis) was significantly lower than during any of the other monitoring periods ($F_{6,24} = 40.99$, $p = 0.0001$). On average, seed predation levels increased consistently from July through September in the partially cut

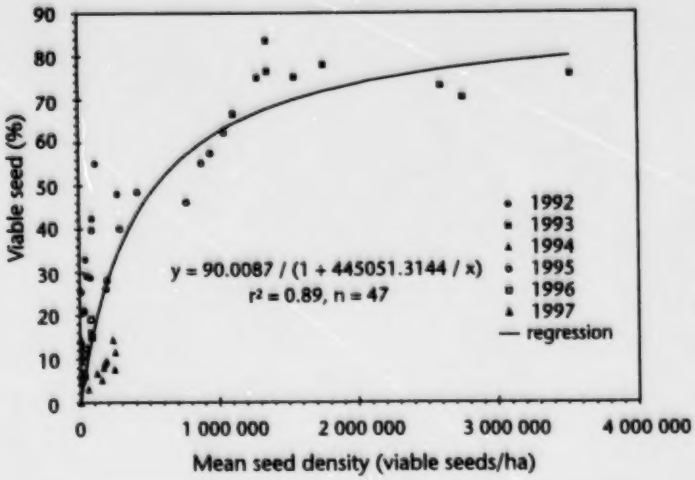

FIGURE 7 *Relationship of percent viable seed to the size of the annual seed crop in Douglas-fir.*

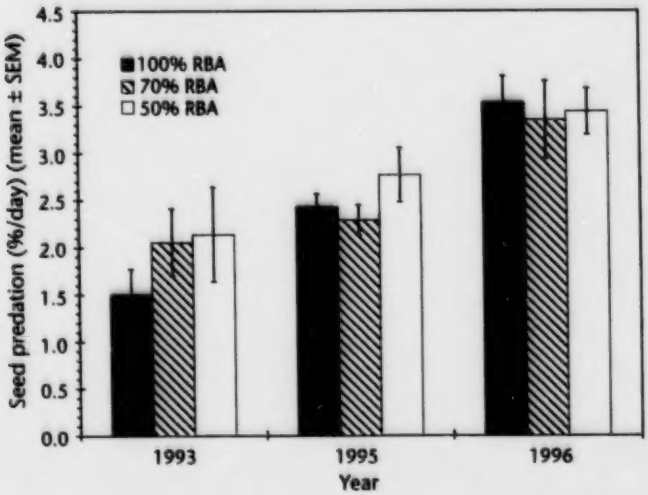

FIGURE 8 *Mean rates of Douglas-fir seed loss to small mammals under each cutting treatment in each of 4 years, all three locations combined. No seed predation monitoring was conducted in 1994. (rba = residual basal area.)*

treatments, though they stayed relatively constant in the uncut control stands (Figure 9). Evaluated over a single period of approximately 6 months, average levels of seed predation during the winter months were very low (<0.4 %/day) under all treatments.

Seed predation under different canopy treatments was not consistent from year to year. However, over all monitoring intervals, average predation levels in partially cut treatments (2.56%/day and 2.71%/day under 70% RBA and 50% RBA treatments, respectively) were significantly greater than in the 100% RBA units (2.37%/day) but not different from each other ($F_{2,52} = 7.77$, $p = 0.0011$).

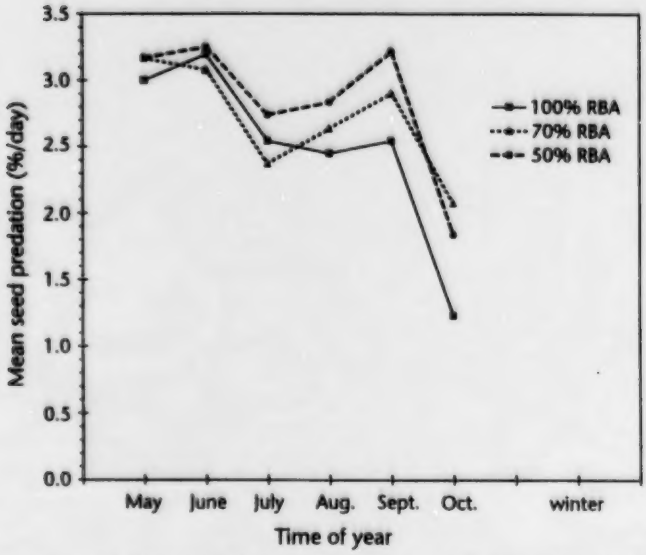

FIGURE 9 *Seasonal trends in seed predation under different residual basal area (rba) treatments, averaged from October 1992 to October 1993 and from May 1995 to September 1996, all three locations combined.*

3.5 Seedbed Distribution

Sampling prior to harvest confirmed that there were no significant differences in mean forest floor thickness among the units slated for different treatments (data not shown). There was, however, a significant ($F_{2,8} = 8.89$, $p = 0.0093$) difference among the three locations: duff thickness at Beedy Creek averaged 6.4 cm, which was significantly greater than at Gavin Road (4.4 cm) and at the UBC Research Forest (4.1 cm). No pre-harvest survey was conducted to describe the cover of different seedbed materials in different treatment units.

The broad cover classes used for the seedbed survey conducted in 1991, immediately after harvest, had less resolution than those sampled similarly in 1993. However, since the surveys in 1991 and 1993 recognized the same four seedbed categories and employed the same 50 m^2 sample plots, results can be compared in terms of the frequency of plots in which each type of seedbed was found. Immediately after harvesting, disturbed forest floor was much more abundant (found in >41% of all subplots) in all of the logged units than in the uncut units (found in <7% of the plots; Figure 10a). The incidence of rotting wood was likewise much greater (>27% frequency) in the harvested units than in the uncut units (1.7% frequency; Figure 10b). Mineral soil apparently increased from 5.2% (as found in the uncut units) to 13–16% frequency in the light cutting treatments, and to 23–35% in the heavy removal treatments (Figure 10c).

When resampled in 1993, less than 5% of the plots had forest floor or moss layers that were recognized as disturbed (Figure 10a). There also seems to have been some breakdown of exposed rotting wood (Figure 10b) and regrowth of vegetation on mineral soil (Figure 10c), because both decreased in frequency in all harvested units from 1991 to 1993. Rotting wood was anomalously more abundant in uncut treatment units in 1993 than in 1991 (Figure 10b). Exposed mineral soil remained more abundant (>18%) in units with 50% RBA than in those having 30% RBA (where mineral soil declined to <8%; Figure 10c).

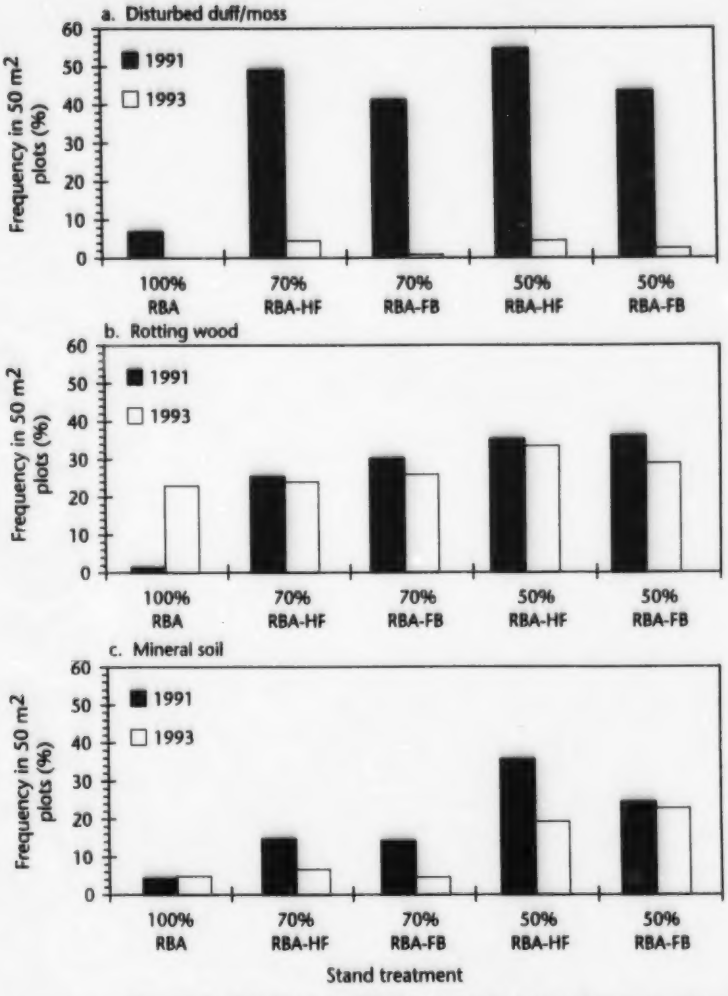

FIGURE 10 *Occurrence of suitable seedbeds—(a) disturbed duff or moss, (b) rotting wood, and (c) mineral soil—under different stand treatments in 1991 and 1993, based on their frequency in a total of forty five 50 m² plots, all three locations combined.*

More precise 1993 estimates of seedbed cover within sample plots better emphasized the prevalence of undisturbed forest floor in all treatments (Table 5). Plots in all treatment units were dominated by undisturbed forest floor (>91% cover), with other substrates each making up less than 7% cover. Analysis of variance conducted on arc-sine square-root transformed data indicates that only mineral soil varied significantly ($F_{4,8} = 5.91$, $p = 0.016$) among treatments, being most abundant where 50% basal area removal was achieved with a feller-buncher. Planned contrasts also confirmed that 50% RBA treatments exposed significantly more mineral soil than 70% RBA treatments ($F = 16.72$, $p = 0.0035$); feller-buncher versus hand-falling contrasts were not significant. These differences remain minor, however: 2.2 ± 1.2% mineral soil cover in 50% RBA-FB units, compared to 0.4 ± 0.1% mineral soil cover in control units (Table 5).

A still more detailed seedbed survey (conducted during the fall of 1993 only in those units logged by feller-buncher or left uncut) distinguished

TABLE 5 *Percent cover (mean ± S.E.M., rounded to two significant digits) of different seedbed materials assessed during regeneration surveys in 1993 (Year 2 post-treatment), analyzed for treatment effects across all three locations*

	Treatment*					ANOVA results	
Substrate	100% RBA	70% RBA-HF	70% RBA-FB	50% RBA-HF	50% RBA-FB	$F_{4,8}$	Prob.>F†
Undisturbed duff/moss	98±1	92±3	93±3	93±3	93±2	2.98	0.088
Disturbed duff/moss	0	1.2±0.6	0.02±0.02	0.33±0.33	0.58±0.58	1.09	0.42
Rotting wood	2.0±1.1	6.5±2.9	6.5±3.0	6.1±2.5	4.6±1.2	2.78	0.10
Mineral soil	0.37±0.10	0.43±0.30	0.14±0.07	0.78±0.10	2.2±1.2	5.91	**0.016**
	ab	ab	b	ab	a		

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed seed densities followed by Scheffé's multiple comparison tests; means in the same line subtended by the same letter are not significantly different at the p = 0.05 level. **Bold** numbers indicate statistically significant results.

* Treatments denoted by: RBA = residual basal area; HF = harvested by hand-falling; FB = harvested by feller-buncher.

† Prob.>F values are rounded to two significant digits. Treatment effects are significant at the 95% confidence level if Prob.<0.05.

between living moss and forest floor substrates and confirmed that seedbed conditions were largely similar among the three locations. Live moss cover was significantly lower ($F_{2,4}$ = 24.71, p = 0.0056) in the 50% RBA units than in the 100% RBA (control) units (Figure 11). Intact forest floor categories were marginally lower in the harvested units too, while disturbed forest floor seedbeds have marginally increased as a result. Likewise, the amount of exposed rotten wood has increased marginally ($F_{2,4}$ = 6.58, p = 0.054), being greater in the 70% RBA treatments than in the uncut 100% RBA units when evaluated at the p = 0.10 significance level. Woody debris makes up most of the "other" category as well, with logging slash especially prevalent in the harvested units. More than 42% of the ground's surface is completely unsuitable for seed germination and seedling growth after logging (even when limbing and

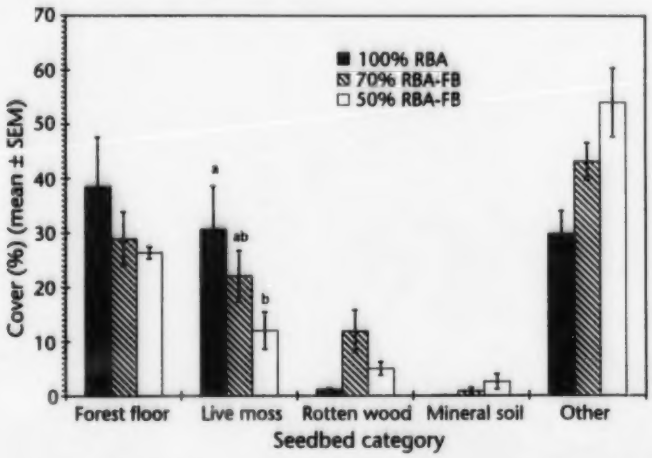

FIGURE 11 *Abundance of general seedbed categories in autumn 1993, all years and locations combined. Columns sharing the same letter are not significantly different at the p = 0.05 level; other seedbeds exhibited no significant differences among treatments.*

topping is conducted at the landing, as in the feller-buncher treatment units), compared to approximately 30% of the ground area being so excluded in the uncut units (Figure 11).

3.6 Seed Germination

If one excludes the confounding influence of any plots subject to animal disturbance and the 0% RBA (clearcut) treatments tested only in 1996, all tree species tested showed remarkable similarity in their overall patterns of germination. Within each species, the highest rates of germination were observed in 1996, followed by 1994, with the lowest rates in 1995 (Figure 12). Germination in 1996 averaged 33% for Douglas-fir, 21% for hybrid white spruce, 28% for lodgepole pine, and 25% for subalpine fir (Figure 12).

Germination of all four conifer species responded much more strongly to seedbed treatments than to canopy treatments or the interaction of seedbed and canopy effects. Substrate (seedbed) effects were significant to the germination of all four species in each year tested. Across all 3 years of testing, the variance attributable to substrate ranged from 16.0% (subalpine fir) to 34.0% (hybrid white spruce) (Appendix 1, Table A1.1). This compares with only 0.4% (subalpine fir) to 3.6% (lodgepole pine) of the variance being attributable to direct canopy effects, which were not significant to any species in any year. Interactive effects of substrate and canopy influence were significant to subalpine fir in 1995 and 1996, and to lodgepole pine, hybrid white spruce, and Douglas-fir in 1996, though only 2.7% (hybrid white spruce) to 5.6% (subalpine fir) of the variance in germination is attributable to substrate and canopy interaction (Table A1.1).

Over all 3 years, germination of all four species was best on rotting wood, followed by mineral soil, forest floor, and moss (Figure 13). The difference in germination success on rotting wood and on soil was not significant for any species. While rotting wood was always a significantly superior seedbed to forest floor and moss, germination on mineral soil was significantly greater than on forest floor only for subalpine fir. Germination on mineral soil was always significantly higher than on moss mats. Germination differences between forest floor and moss mats were not significant for any species.

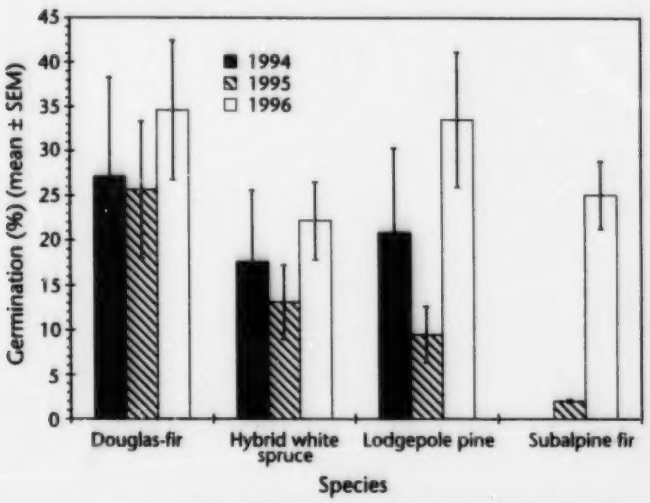

FIGURE 12 *Year-to-year differences in overall germination by each tree species, all stand treatments, seedbeds, and locations combined.*

No species exhibited significant differences in germination among canopy removal treatments (Appendix 1, Table A1.1). Nevertheless, some complex substrate × canopy interaction effects were evident in some species. Douglas-fir germination on rotting wood or mineral soil in clearcuts and on wood under intact canopies was superior, followed by its germination on wood in the partial cutting treatments (Figure 14). The poorest germination of Douglas-fir was found on moss mats in all treatment units, and on forest floor under 50% RBA. Almost identical trends were exhibited by lodgepole pine, hybrid white spruce, and subalpine fir (data not shown), though differences in spruce germination were explainable solely in terms of seedbed effects.

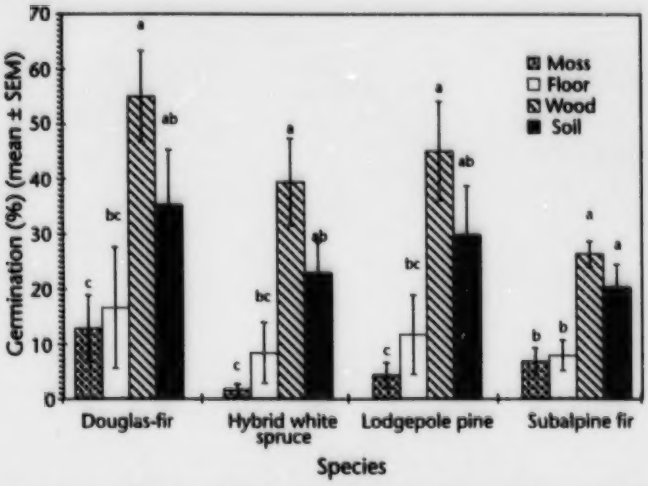

FIGURE 13 *Mean germination of each tree species on different seedbeds, averaged over all years, locations, and stand treatments. Columns within the same species that share the same letter are not significantly different at the p = 0.05 level.*

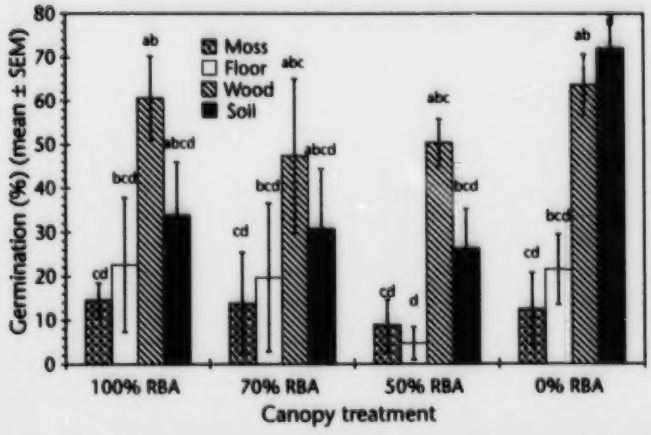

FIGURE 14 *Mean germination of Douglas-fir on different seedbeds under different canopy removal treatments, all locations and years combined. Across all treatment combinations, columns sharing the same letter are not significantly different at the p = 0.05 level.*

3.7 Germinant Survival

Species differences and year-to-year differences in the survival of newly germinated tree seedlings during their first year of growth were much less pronounced than differences observed in germination. When the newly added 0% RBA treatments and any plots subject to disturbance by animals are excluded, average survival in 1996 was found to be equal to or somewhat greater than that in previous years for all five species. Survival during the 1996 growing season averaged 70% for newly germinated seedlings of Douglas-fir, 63% for hybrid white spruce, 57% for lodgepole pine, and 65% for subalpine fir (Figure 15). First-year survival of Douglas-fir (59%) and hybrid white spruce (48%) was lowest in 1994, while that of lodgepole pine (43%) was lowest in 1995. Early survival by subalpine fir germinants in 1995 (64%) was very similar to their survival in 1996.

Treatment effects explained much less of the variance in survival of all conifer species (Appendix 1, Table A1.2) than that observed for germination (Table A1.1). Unlike the germination response, survival was influenced more equally by both canopy and substrate effects (though substrate effects were still more pronounced) for all species except subalpine fir. Neither substrate nor canopy effects were significant (at the $p = 0.05$ level) to the survival of any species in 1994 or 1995, while substrate effects were significant to all species in 1996, and canopy effects were significant to two species in 1996. Douglas-fir survival in 1996 showed significant substrate effects (explaining 9.1% of the variance), while canopy effects were not significant and explained only 6.7% (Table A1.2). Hybrid white spruce survival in 1996 showed significant substrate effects (explaining 18.5% of the variance), greater than the (non-significant) canopy effects, which explained only 1.8% of the variance. Lodgepole pine survival in 1996 was similarly affected by substrate, which accounted for 21.3% of the variance, while canopy effects explained only 1.6% of the variance. Both treatment factors were significant to subalpine fir survival in 1996, with 20.5% of the variance attributable to substrate and 12.5% attributable to canopy effects (Table A1.2).

Assessed over all 3 years, survival of all five species was clearly superior (>54%) on rotting wood and mineral soil (Figure 16). Douglas-fir and subalpine fir, the two species with the largest seeds, also survived equally well on

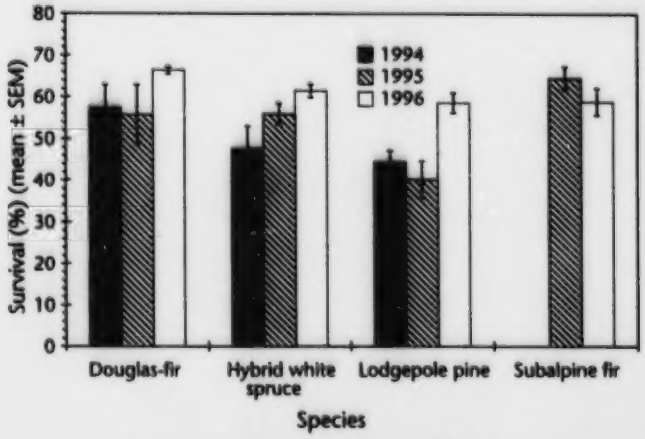

FIGURE 15 *Year-to-year differences in overall first-year survival of newly germinated seedlings of each species tested, all seedbeds and stand treatments combined.*

forest floor substrates (Figure 16). Survival of most species was intermediate on forest floor, while moss mats were universally inferior, supporting mean survival levels of only 21% (lodgepole pine) to 43% (Douglas-fir) (Figure 16).

Surprisingly, most species exhibited no significant differences in survival among canopy removal treatments (Table A1.2). Only subalpine fir in 1996 (and over both years) (Figure 17) exhibited significant survival differences among canopy treatments, showing significantly poorer survival under 100% canopy removal than under any degree of canopy retention. Lodgepole pine survived poorly in uncut control plots, but not significantly less than under other treatments.

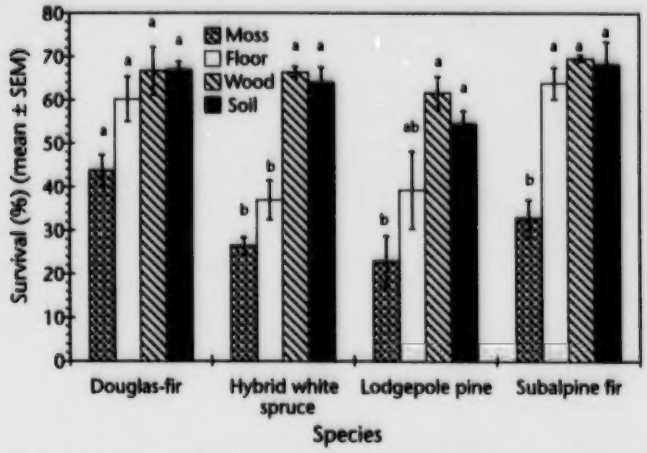

FIGURE 16 *Mean first-year survival of new germinants of each tree species on different seedbeds, all stand treatments, locations, and years combined. Columns within the same species that share the same letter are not significantly different at the p = 0.05 level.*

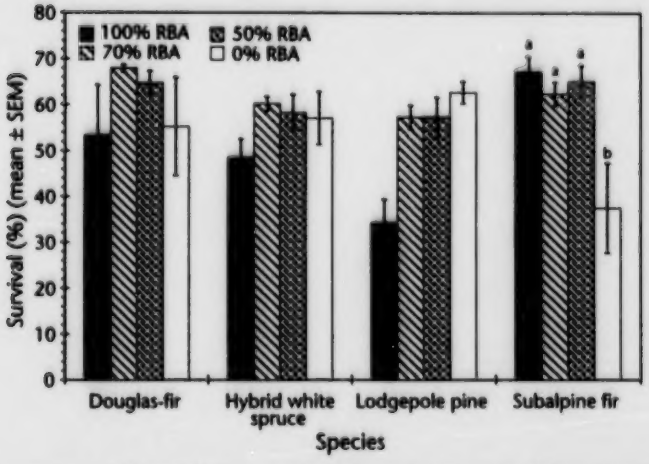

FIGURE 17 *Mean first-year survival of germinants under different canopy treatments, all years and locations combined. Columns within the same species that share the same letter are not significantly different at the p = 0.05 level; no other species differed among treatments. (RBA = residual basal area.)*

Only the survival of Douglas-fir in 1996 (and consequently over all years) showed significant substrate × canopy interaction effects. Mineral soil in the 50% RBA and 0% RBA treatment units supported the best overall Douglas-fir survival, while moss mats in 50% RBA and 0% RBA treatments had the poorest survival (Figure 18). The suitability of moss and forest floor substrates for Douglas-fir survival was greatest under 30% removal, while that of mineral soil was poorest in the uncut control plots (Figure 18).

3.8 Natural Regeneration Densities

3.8.1 Frequency analysis by density class: 1990 and 1991 The first 2 years (1990 and 1991) of regeneration surveys associated with this experiment recorded the abundance of seedlings and poles in broad density classes (Table 1). Though lacking in precision, the tabulation of regeneration by density class can be done rapidly and facilitates the detection of gross differences in density. The use of density classes prohibits the summation of size classes within each species or the summation of all species within each size class.

Regeneration frequencies of each size class of the different conifer species in 1990, prior to logging, are summarized for each of the five harvesting treatments in Table 6, pooled over the three locations studied. Douglas-fir was clearly the most abundant species at all sites, followed by subalpine fir and then by hybrid white spruce, with only three western redcedar and two lodgepole pine seedlings encountered (data not shown). Large seedlings (5.1 –100 cm tall) were more abundant than small seedlings or poles. Many of the sampled plots had no seedlings of one or all species. In general, seedling distributions in 1990 showed clustering and hence a sporadic distribution. Quite by chance, there were slightly more sample plots containing spruce and Douglas-fir seedlings (both small and large) in the treatment units designated for logging than in those units left as controls.

Contingency table analysis tested for both main effects and interaction effects, but the treatment × location interaction was not significant for any species or size class in either 1990 or 1991. When assessed using a main effects model, no species or size class of regeneration was found to vary significantly

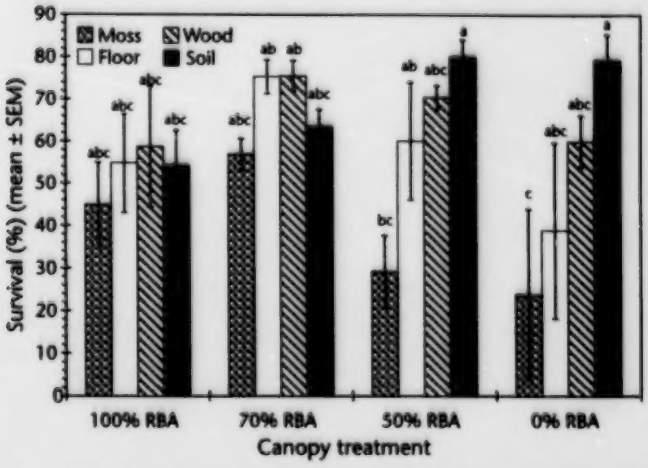

FIGURE 18 *Mean first-year survival of Douglas-fir germinants on different seedbeds under different canopy treatments, all years and locations combined. Across all treatment combinations, columns sharing the same letter are not significantly different at the p = 0.05 level.*

TABLE 6 *Summary of 1990 (pre-treatment) regeneration frequency per 30 sample plots*

Species	Planned treatment: residual basal area	Size class†	Density class*						Density > 0	
			0	1	2	3	4	5	Plots	%
Douglas-fir	100% (control)	small	8	2	5	3	3	9	22	73
		large	4	5	5	5	1	10	26	87
		poles	29	1	0	0	0	0	1	3
	70%, hand-falling	small	8	4	4	2	1	11	22	73
		large	2	7	3	2	7	9	28	93
		poles	28	2	0	0	0	0	2	7
	70%, feller-buncher	small	6	4	5	4	5	6	24	80
		large	1	3	6	3	3	14	29	97
		poles	22	2	2	3	0	1	8	27
	50%, hand-falling	small	4	6	2	8	4	6	26	87
		large	1	4	4	2	5	14	29	97
		poles	28	2	0	0	0	0	2	7
	50%, feller-buncher	small	2	4	3	12	6	3	28	93
		large	1	2	3	4	4	16	29	97
		poles	20	6	2	0	2	0	10	33
Hybrid white spruce	100% (control)	small	29	1	0	0	0	0	1	3
		large	19	9	2	0	0	0	11	37
		poles	29	1	0	0	0	0	1	3
	70%, hand-falling	small	29	1	0	0	0	0	1	3
		large	15	10	3	2	0	0	15	50
		poles	24	5	1	0	0	0	6	20
	70%, feller-buncher	small	28	1	1	0	0	0	2	7
		large	12	9	6	3	0	0	18	60
		poles	18	5	5	2	0	0	12	40
	50%, hand-falling	small	28	2	0	0	0	0	2	7
		large	18	8	2	1	0	1	12	40
		poles	27	3	0	0	0	0	3	10
	50%, feller-buncher	small	28	1	1	0	0	0	2	7
		large	8	14	5	2	0	1	22	73
		poles	16	11	1	1	1	0	14	47
Subalpine fir	100% (control)	small	30	0	0	0	0	0	0	0
		large	11	17	0	2	0	0	19	63
		poles	25	4	0	1	0	0	5	17
	70%, hand-falling	small	28	2	0	0	0	0	2	7
		large	14	9	4	2	1	0	16	53
		poles	19	7	1	3	0	0	11	37
	70%, feller-buncher	small	30	0	0	0	0	0	0	0
		large	7	11	3	8	0	1	23	77
		poles	13	6	6	3	2	0	17	57
	50%, hand-falling	small	30	0	0	0	0	0	0	0
		large	12	13	3	1	1	0	18	60
		poles	20	7	2	1	0	0	10	33
	50%, feller-buncher	small	30	0	0	0	0	0	0	0
		large	7	16	4	2	1	0	23	77
		poles	18	8	2	2	0	0	12	40

* Density classes: 0 = 0 stems per 50 m^2 plot (0 stems/ha); 1 = one to three stems per plot (200–600 stems/ha); 2 = four to seven stems per plot (800–1400 stems/ha); 3 = eight to 19 stems per plot (1600–3800 stems/ha); 4 = 20 to 39 stems per plot (4000–7800 stems/ha); and 5 = 40+ stems per plot (>8000 stems/ha).

† Size classes: small = ≤5.0 cm tall; large = 5.1–100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

among treatment blocks prior to harvest (Table 7). Location effects, on the other hand, showed several pre-treatment differences, with small and large Douglas-fir regeneration being more abundant at the Beedy Creek site than at Gavin Road or the UBC Research Forest (Table 7). Those treatment units supporting significantly higher or lower densities of seedlings need to be kept in mind when evaluating post-treatment regeneration densities.

Regeneration frequencies in 1931 (Table 8) were very similar to those in 1990. Douglas-fir, the most abundant species, decreased markedly from pre-treatment levels in all harvested plots. Apparently, all Douglas-fir poles in the permanent sample plots were destroyed by harvesting activities or recent snow breakage, and the frequency of plots with seedlings decreased by an average of 23% in the harvested units compared to a decrease of 6% in the control units. Contingency table analysis of main effects (Table 9) reveals no significant treatment effects on the distribution of regeneration in 1991. Large Douglas-fir seedlings, though not small seedlings, remained significantly more abundant at Beedy Creek; small Douglas-fir seedlings were now less frequent than expected at the UBC site.

3.8.2 **Regeneration densities: 1993–1996** None of the harvested treatment units supported significantly greater densities (at the $p = 0.05$ significance level) of natural regeneration than those found in the control units in 1993 (Table 10). Planned contrasts revealed a few treatment differences, however, especially with respect to the distribution of large and pole-sized regeneration. Units logged by feller-buncher supported significantly greater densities of spruce poles ($F_{2,8} = 6.87$, $p = 0.031$), and marginally greater densities of Douglas-fir ($F_{2,8} = 4.46$, $p = 0.068$) and subalpine fir ($F_{2,8} = 3.83$, $p = 0.086$) poles than units logged by hand-falling. Planned contrasts also indicate that the density of subalpine fir poles was significantly greater in the 70% RBA units than in the 50% RBA units ($F_{2,8} = 6.82$, $p = 0.031$).

TABLE 7 *Contingency table analysis of the frequency of six classes of regeneration density observed under the five different treatments and three locations in 1990 (pre-treatment)**

Species	Size class†	Treatment effect, d.f.=20 Chi-square	Prob.‡	Higher in:	Location effect, d.f.=10 Chi-square	Prob.‡	Higher in:	Treat. x loc., d.f.=40 Chi-square	Prob.‡
Douglas-fir	small	28.34	0.10	-	49.03	<0.0001	Beedy	50.47	0.12
	large	21.33	0.38	-	48.91	<0.0001	Beedy	42.52	0.36
	poles	16.23	0.70	-	12.23	0.27	-	21.11	0.99
Hybrid white spruce	small	1.73	1.00	-	4.40	0.94	-	7.58	1.00
	large	14.74	0.79	-	20.15	0.028	-	20.34	1.00
	poles	22.32	0.32	-	5.78	0.83	-	20.47	1.00
Subalpine fir	small	2.17	1.00	-	1.43	1.00	-	0.46	1.00
	large	19.42	0.49	-	18.37	0.049	-	24.76	0.97
	poles	14.09	0.83	-	4.34	0.93	-	30.81	0.85

Note: **Bold** numbers indicate statistically significant results.

* Based on the results partially summarized in Table 6 (but retaining individual location results), with SAS procedure CATMOD using a log-linear model and maximum likelihood estimation. Interaction effects are reported, but none was significant, so the treatment and location effects are from main effects models. SAS procedure FREQ was then used to determine the contribution of each cell to total chi-square in treatment x density class and location x density class contingency tables, thereby indicating significantly ($p = 0.05$) higher or lower treatments or locations.

† Size classes: small = ≤5.0 cm tall; large = 5.1 100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

‡ If Prob. <0.05 then the effect is significant at the 95% level of confidence.

TABLE 8 *Summary of 1991 (Year 0 post-treatment) regeneration frequency per 30 plots*

Species	Treatment: residual basal area	Size Class*	Density class†						Density > 0	
			0	1	2	3	4	5	Plots	%
Douglas-fir	100% (control)	small	9	6	6	3	3	3	21	70
		large	6	1	4	7	2	10	24	80
		poles	25	5	0	0	0	0	5	17
	70%, hand–falling	small	13	4	5	7	1	0	17	57
		large	6	6	4	5	6	3	24	80
		poles	30	0	0	0	0	0	0	0
	70%, feller-buncher	small	14	3	6	6	0	1	16	53
		large	3	5	3	4	8	7	27	90
		poles	30	0	0	0	0	0	0	0
	50%, hand–falling	small	14	8	5	1	1	1	16	53
		large	4	3	6	6	5	6	26	87
		poles	30	0	0	0	0	0	0	0
	50%, feller-buncher	small	16	8	1	1	4	0	14	47
		large	3	5	2	9	6	5	27	90
		poles	30	0	0	0	0	0	0	0
Hybrid white spruce	100% (control)	small	30	0	0	0	0	0	0	0
		large	16	11	3	0	0	0	14	47
		poles	29	1	0	0	0	0	1	3
	70%, hand–falling	small	29	0	1	0	0	0	1	3
		large	19	8	1	2	0	0	11	37
		poles	30	0	0	0	0	0	0	0
	70%, feller-buncher	small	26	4	0	0	0	0	4	13
		large	15	9	2	4	0	0	15	50
		poles	29	1	0	0	0	0	1	3
	50%, hand–falling	small	29	1	0	0	0	0	1	3
		large	19	7	3	0	1	0	11	37
		poles	30	0	0	0	0	0	0	0
	50%, feller-buncher	small	27	3	0	0	0	0	3	10
		large	11	11	6	1	1	0	19	63
		poles	29	1	0	0	0	0	1	3
Subalpine fir	100% (control)	small	29	1	0	0	0	0	1	3
		large	13	10	5	1	1	0	17	57
		poles	30	0	0	0	0	0	0	0
	70%, hand–falling	small	29	1	0	0	0	0	1	3
		large	16	5	3	5	1	0	14	47
		poles	30	0	0	0	0	0	0	0
	70%, feller-buncher	small	30	0	0	0	0	0	0	0
		large	6	9	8	4	2	1	24	80
		poles	30	0	0	0	0	0	0	0
	50%, hand–falling	small	29	1	0	0	0	0	1	3
		large	14	11	3	2	0	0	16	53
		poles	30	0	0	0	0	0	0	0
	50%, feller-buncher	small	30	0	0	0	0	0	0	0
		large	11	14	2	2	1	0	19	63
		poles	29	1	0	0	0	0	1	3

* Size classes: small = ≤5.0 cm tall; large = 5.1–100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

† Density classes: 0 = 0 stems per 50 m^2 plot (0 stems/ha); 1 = one to three stems per plot (200–600 stems/ha); 2 = four to seven stems per plot (800–1400 stems/ha); 3 = eight to 19 stems per plot (1600–3800 stems/ha); 4 = 20 to 39 stems per plot (4000–7800 stems/ha); and 5 = 40+ stems per plot (>8000 stems/ha).

TABLE 9 *Contingency table analysis of the frequency of six classes of regeneration density observed under the five different treatments and three locations in 1991 (immediately after treatment)**

		Treatment effect, d.f.=20				Location effect, d.f.=10				Treat. x loc., d.f.=40	
Species	Size class†	Chi-square	Prob.‡	Lower in:	Higher in:	Chi-square	Prob.	Lower in:	Higher in:	Chi-square	Prob.
Douglas-fir	small	25.52	0.18	-	-	49.54	<0.0001	UBC	-	44.03	0.30
	large	23.57	0.26	-	-	40.19	<0.0001	-	Beedy	39.25	0.50
	poles	3.47	1.00	-	-	1.21	1.00	-	-	0.04	1.00
Hybrid white spruce	small	5.96	1.00	-	-	3.83	0.95	-	-	0.74	1.00
	large	9.99	0.97	-	-	8.73	0.56	-	-	12.80	1.00
	poles	0.69	1.00	-	-	0.25	1.00	-	-	5.63	1.00
Subalpine fir	small	0.92	1.00	-	-	0.16	1.00	-	-	4.34	1.00
	large	14.05	0.83	-	-	7.34	0.69	-	-	21.91	0.99
	poles	1.10	1.00	-	-	0.58	1.00	-	-	0.32	1.00

Note: **Bold** numbers indicate statistically significant results.

* Based on the results partially summarized in Table 8 (but retaining individual location results), with SAS procedure CATMOD using a log-linear model and maximum likelihood estimation. Interaction effects are reported, but none was significant, so the treatment and location effects are from main effects models. SAS procedure FREQ was then used to determine the contribution of each cell to total chi-square in treatment x density class and location x density class contingency tables, thereby indicating significantly ($p = 0.05$) higher or lower treatments or locations.

† Size classes: small = ≤5.0 cm tall; large = 5.1 100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

‡ If Prob. <0.05 then the effect is significant at the 95% level of confidence.

Table 11 summarizes the raw density data from 1994, along with the results of analyses of variance on each size class of each species, and on all size classes and species combined. Densities of all species, across all treatments, were approximately three to 11 times those encountered in 1993, though pole densities were relatively unchanged. As in 1990 and 1993, more subalpine fir poles were counted in the 70% RBA-FB plots than in the unlogged units, while none of the other species showed any significant treatment differences (Table 11). This was further confirmed by the planned contrasts, which found poles of subalpine fir to be significantly more abundant in 70% RBA treatments than in 50% RBA treatments ($F_{2,8} = 9.79$, $p = 0.014$) and significantly more abundant in feller-buncher than hand-felled units ($F_{2,8} = 5.42$, $p = 0.048$). Large seedlings of subalpine fir were also more abundant in 70% RBA than 50% RBA units ($F_{2,8} = 5.94$, $p = 0.041$), and poles of hybrid white spruce were more abundant in units logged by feller-buncher than by hand ($F_{2,8} = 6.50$, $p = 0.034$).

Regeneration densities of all species in 1996 (Table 12) averaged 9–39% of those observed in 1994. Because sampling procedures were exactly the same, this difference over 2 years cannot be considered an artifact of sampling methodologies. Analysis of variance shows even fewer treatment effects on regeneration densities in 1996 than those observed in 1994. Only some incidental occurrences of lodgepole pine seedlings in the harvested units were significantly different among treatments (Table 12). For medium (10.1–30 cm tall) lodgepole pine seedlings, greater densities were observed in the 50% RBA-FB units than in any of the other treatment units. Significant planned contrasts were also found only for these medium lodgepole pine seedlings ($F_{2,8} = 8.00$, $p = 0.022$), which can be interpreted to indicate 50% RBA as supporting more pine seedlings than 70% RBA, or that feller-buncher units

TABLE 10 *Regeneration densities (mean stems per ha, ± S.E.M.) in 1993, Year 2 post-treatment, comparing treatments across all three locations*

Species	Size class*	Treatment, residual basal area					ANOVA results	
		100%	70%- HF	70%-FB	50%-HF	50%-FB	$F_{4,8}$	Prob.>F†
Douglas-fir	small	2618±1815	2093±1720	720±576	773±576	911±317	0.63	0.66
	large	13547±10148	7182±4838	9098±5528	9018±5210	8396±4853	0.50	0.74
	poles	49±24	27±13	813±568	80±43	524±518	1.44	0.31
	all	16213±11953	9302±6563	10631±6593	9871±5489	9831±5179	0.46	0.76
Hybrid white spruce	small	0	13±13	0	13±13	9±4	0.97	0.47
	large	222±117	276±198	400±185	444±365	444±237	2.89	0.094
	poles	84±50	62±36	262±136	80±34	262±178	1.17	0.39
	all	307±160	351±247	662±308	538±411	716±410	2.91	0.093
Lodgepole pine	small	0	0	0	0	0	-	-
	large	0	13±13	0	0	0	1.00	0.46
	poles	0	0	0	0	0	-	-
	all	0	13±13	0	0	0	1.00	0.46
Subalpine fir	small	0	0	9±4	0	0	4.00	0.045
	large	396±121	813±466	1284±562	676±111	787±318	0.63	0.65
	poles	204±70	418±187	991±242	249±122	311±121	1.75	0.23
	all	600±78	1231±651	2284±728	924±232	1098±214	0.79	0.56
Western redcedar	small	0	0	0	0	0	-	-
	large	0	9±9	0	0	4±4	1.00	0.46
	poles	4±4	36±36	0	4±4	0	1.00	0.46
	all	4±4	44±44	0	4±4	4±4	1.00	0.46
All species combined	small	2618±1815	2107±1733	729±511	787±291	920±320	0.62	0.66
	large	14164±10283	8293±4590	10782±5289	10138±5465	9631±4347	0.32	0.86
	poles	342±131	542±151	2067±508	413±69	1098±813	1.91	0.20
	all	17124±12163	10942±6170	13578±6210	11338±5690	11649±5463	0.39	0.81

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed data, followed by Scheffé's multiple comparison tests, none of which was significant at the p = 0.05 confidence level. **Bold** numbers indicate statistically significant results.

* Size classes: small = ≤5.0 cm tall; large = 5.1 100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

† If Prob. <0.05 then the treatment effect is significant at the 95% level of confidence.

supported more pine seedlings than hand-felled units. As in previous years, large seedlings of subalpine fir were significantly more abundant in the 70% RBA treatments than in the 50% RBA treatments. Large seedlings of hybrid white spruce remained more abundant in the units logged by feller-buncher than in those logged by hand-falling ($F_{2,8} = 5.42$, $p = 0.048$), and pole-sized Douglas-fir were likewise more abundant in the feller-buncher logged units ($F_{2,8} = 6.52$, $p = 0.034$). Five years after the harvesting treatments, new seedlings of Douglas-fir (the main crop species for which this silvicultural trial was initiated) showed remarkably little variation in density among treatments, with seedlings ≤100 cm tall averaging 14 822–18 066 stems per ha under the full range of treatments (including uncut controls).

3.8.3 Multiyear trends Multiyear trends are portrayed solely in terms of changes in mean density, with midpoints of the density classes employed in

TABLE 11 *Regeneration densities (mean stems per ha, ± S.E.M.) in 1994, Year 3 post-treatment, comparing treatments across all three locations*

Species	Size class*	Treatment, residual basal area					ANOVA results	
		100%	70%-HF	70%-FB	50%-HF	50%-FB	$F_{4,8}$	Prob.> F†
Douglas-fir	germinant	160 000±124 134	82 667±52 984	17 778±8695	30 889±12 149	30 667±15 506	2.49	0.13
	small	15 778±10786	14 000±7211	7556±4240	9111±1819	11 778±3135	1.08	0.43
	medium	7644±6094	4244±2218	5867±3800	4867±2034	4956±2598	0.09	0.98
	large	4711±3506	1422±771	6578±5129	3578±2243	7067±6242	3.51	0.062
	pole	49±27	102±42	1013±858	31±25	529±516	1.51	0.29
	all sizes	188 182±14 4458	102 436±62 049	38 791±21 906	48 476±17 432	54 996±27 925	0.22	0.92
Hybrid white spruce	germinant	0	0	0	0	0	-	-
	small	0	0	0	0	889±889	1.00	0.46
	medium	156±124	44±22	156±89	133±133	400±367	1.18	0.39
	large	156±80	0	378±124	267±204	622±523	4.05	**0.044**
	pole	62±35	80±41	298±154	84±40	302±210	2.21	0.16
	all sizes	373±190	124±58	831±329	484±372	2213±1987	4.53	**0.033**
Lodgepole pine	germinant	0	0	0	222±222	0	1.00	0.46
	small	0	222±222	0	222±222	444±444	0.61	0.67
	medium	0	44±44	0	0	22±22	1.00	0.46
	large and pole	0	0	0	0	0	-	-
	all sizes	0	267±204	0	444±444	467±434	0.98	0.47
Subalpine fir	germinant	0	0	0	0	0	-	-
	small	0	0	222±222	0	222±222	0.67	0.63
	medium	222±190	311±244	533±468	311±194	267±139	0.60	0.67
	large	333±38	778±323	978±256	400±252	578±97	3.09	0.082
	pole	191±64	449±203	991±145	204±91	333±113	2.87	0.10
	all sizes	747±95	1538±703	2724±666	916±533	1400±290	2.41	0.13
Western redcedar	germinant and small	0	0	0	0	0	-	-
	medium and large	0	0	0	0	0	-	-
	pole	0	4±4	0	4±4	0	1.00	0.46
	all sizes	0	4±4	0	4±4	0	1.00	0.46
All species combined	germinant	160 000±124 134	82 667±52 984	17 778±8695	31 111±11 928	30 667±15 506	2.48	0.13
	small	15 778±10 786	14 222±7276	7778±4151	9333±1678	13 333±3672	0.98	0.47
	medium	8022±6095	4644±2040	6556±3643	5311±1949	5644±2857	0.31	0.86
	large	5200±3550	2200±454	7933±4927	4244±2205	8267±6676	4.70	**0.030**
	pole	302±118	636±154	2302±1004	324±59	1164±838	2.42	0.13
	all	189 302±144 549	104 369±61 386	42 347±21 559	50 324±16 725	59 076±29 433	0.13	0.97

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed data, followed by Scheffé's multiple comparison tests, none of which was significant at the p = 0.05 confidence level. **Bold** numbers indicate statistically significant results.

* Size classes are: germinant = 1–2 years old; small = others ≤10 cm tall; medium = 10.1–30 cm, tall; large = 30.1–100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

† If Prob.<0.05 then the treatment effect is significant at the 95% level of confidence.

TABLE 12 *Regeneration densities (mean stems per ha, ± S.E.M.) in 1996, Year 5 post-treatment, comparing treatments across all three locations*

Species	Size class*	Treatment, residual basal area					ANOVA results	
		100%	70%-HF	70%-FB	50%-HF	50%-FB	$F_{4,8}$	Prob.>F†
Douglas-fir	germinant	6000±2694	9333±5551	4444±1352	6889±3274	4444±1849	0.11	0.97
	small	6667±5670	5333±2694	5333±2524	6444±1556	6667±3151	0.80	0.56
	medium	2822±1956	2044±908	2511±490	1578±502	1733±269	0.73	0.60
	large	1667±1534	1356±1092	2756±1471	1333±423	1978±1427	2.78	0.10
	pole	49±25	71±32	213±111	27±13	164±151	1.25	0.37
	all	17 204±11557	18 138±9829	15 258±4736	16 271±53851	14 987±2833	0.98	0.47
Hybrid white spruce	germinant	0	222±222	0	0	222±222	1.00	0.46
	small	0	222±222	0	0	222±222	0.67	0.63
	medium	89±44	22±22	44±22	44±22	44±22	0.51	0.73
	large	133±77	0	222±160	44±22	179±111	1.68	0.25
	pole	53±31	44±19	98±65	80±28	147±27	1.39	0.32
	all	276±131	511±203	364±239	169±58	813±594	1.66	0.25
Lodgepole pine	germinant	0	0	222±222	222±222	222±222	0.50	0.74
	small	0	0	0	0	222±222	1.00	0.46
	medium	0	22±22	0	0	111±22	7.21	**0.0092‡**
		b	ab	b	b	a		
	large	0	0	0	0	0	-	-
	pole	0	0	0	0	0	-	-
	all	0	22±22	222±222	222±222	556±456	2.23	0.16
Subalpine fir	germinant	0	0	0	0	0	-	-
	small	0	0	0	0	0	-	-
	medium	89±44	156±156	178±97	44±22	111±59	0.38	0.82
	large	89±59	511±349	400±300	156±80	289±160	3.40	0.066
	pole	53±23	160±114	276±75	76±12	240±43	1.18	0.34
	all	231±65	827±617	853±207	276±82	640±239	1.28	0.35
Western redcedar	germinant	0	0	0	0	0	-	-
	small	0	0	0	0	0	-	-
	medium	0	0	0	0	0	-	-
	large	0	22±22	0	0	0	1.00	0.46
	pole	9±9	27±27	0	22±22	0	1.00	0.46
	all	9±9	49±49	0	22±22	0	1.00	0.46
All species combined	germinant	6000±2694	9556±5765	4667±1155	7111±3205	4889±1819	0.10	0.98
	small	6667±5670	5556±2784	5333±2524	6444±1556	7111±3318	0.73	0.60
	medium	3000±1935	2244±770	2733±444	1667±473	2000±333	2.45	0.13
	large	1889±1595	1889±873	3378±1329	1533±346	2444±1414	1.54	0.28
	pole	164±76	302±90	587±159	187±35	551±188	1.75	0.23
	all	17 720±11 604	19 547±9479	16 698±4516	16 942±5282	16 996±3279	0.74	0.59

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed data, followed by Scheffé's multiple comparison tests; means in the same line subtended by the same letter are not significantly different at the p = 0.05 confidence level.

* size classes are: germinant = 1–2 years old; small = others ≤10 cm tall; medium = 10.1–30 cm tall; large = 30.1–100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

† If Prob.<0.05 then the treatment effect is significant at the 95% confidence level.

‡ Numbers which are bold indicate statistically significant results.

1990 and 1991 used to estimate the mean regeneration densities (in stems per ha) for each treatment unit, as summarized in Appendix 2. All species in all partially cut treatment units decreased in estimated density from 1990 (pre-harvest) to 1991 (immediately after harvest). Densities from 1991 to 1993 remained quite stable or increased slightly. Most species then experienced a marked increase in density in some treatment units in 1994, though some species in other units remained constant or declined somewhat. Regeneration densities in 1996 were then generally lower than in 1994, though not as low as in 1993 or previous years.

Douglas-fir regeneration showed the most dynamic changes from year to year, spanning three orders of magnitude over the 7 years surveyed (Figure 19). As with seed rain, results were strongly influenced by prolific reproduction in the Beedy Creek stand, which frequently masked treatment differences. Treatments resulted in remarkably little difference in overall densities in any given year, with control units supporting the greatest number of seedlings from 1991 to 1994. Starting during the high-density year of 1994, the 70% RBA-HF units emerged as supporting more seedlings than the other partially cut units, and subsequently surpassed the control units in 1996 (Figure 19).

Hybrid white spruce regeneration densities were much less than those of Douglas-fir, and fluctuated less over time (Figure 20). Seedling densities remained stable from 1991 to 1993, with the rank order of treatments unchanged from pre-harvesting conditions. A marked divergence in treatments was then evident in 1994, with densities increasing in 50% RBA-FB and decreasing in 70% RBA-HF units. The latter treatment then jumped to support the second-highest density of seedlings in 1996, while 50% RBA-HF treatments continued their decline to support the lowest density in 1996 (Figure 20). Densities in the 50% RBA-HF units remained the highest, as they were prior to logging.

The density of subalpine fir seedlings was generally similar to that of hybrid white spruce, but remained relatively unchanged from 1990 to 1996 (Figure 21). The most pronounced change over time has been the 1996 decline in subalpine fir seedling densities in the 70% RBA-FB units (Figure 21).

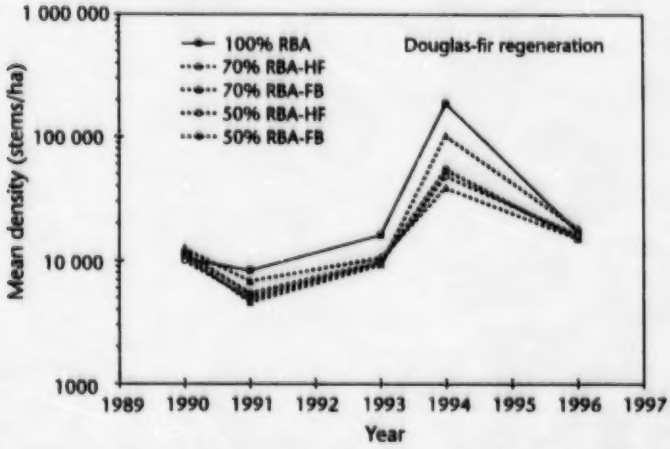

FIGURE 19 *Trends in estimated Douglas-fir regeneration density over 7 years, all size classes and locations combined.*

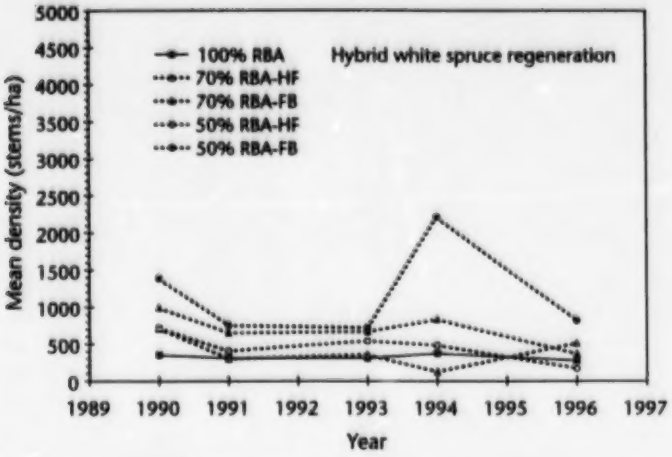

FIGURE 20 *Trends in estimated hybrid white spruce regeneration density over 7 years, all size classes and locations combined.*

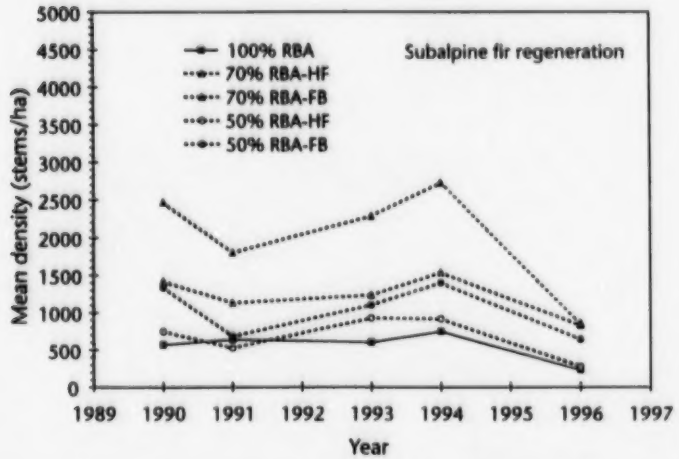

FIGURE 21 *Trends in estimated subalpine fir regeneration density over 7 years, all size classes and locations combined.*

When evaluated over all years sampled, few species showed significant overall responses to any of the treatments. Planned contrasts showed that large hybrid white spruce seedlings were more abundant in the feller-buncher units than in the hand-falling units ($F_{1,10} = 5.67$, $p = 0.039$). Subalpine fir poles were likewise more abundant in the feller-buncher treatment units ($F_{1,10} = 5.73$, $p = 0.038$). Regeneration of that size would have been present prior to harvesting, and does not represent establishment stimulated by the harvesting treatments. Douglas-fir regeneration of all sizes showed no significant all-year response to the harvesting treatments.

In order to better portray the dynamics of "new" Douglas-fir seedlings, an effort was made to identify the subset of the total regeneration sampled in each year that likely germinated since harvesting in 1991. For these purposes, we assume that all germinants (<2 years old) and all small seedlings (≤10 cm tall) detected in 1993 or thereafter clearly originated after harvesting. Based

on average growth rates estimated for natural regeneration (3–4 cm/yr) (Section 3.9), however, it is likely that a number of seedlings that germinated in the spring of 1992 were up to 8 cm tall when sampling was conducted in 1993. To account for this possibility, 3/95 (3 cm / 95 cm = 0.032) of the medium-sized seedlings (5.1–100 cm tall) were added to the small seedlings (Table 1) to define "new seedlings" at the time of monitoring in 1993. (This assumes a uniform age class structure within each size class.) Likewise, some 1992 germinants were probably up to 12 cm tall in 1994 and 20 cm tall in 1996, so 2/20 (2 cm / 20 cm = 0.10) of the medium-sized seedlings (10.1–30 cm tall) in 1994 and 10/20 (10 cm / 20 cm = 0.50) of the medium-sized seedlings in 1996 were added to the germinants and small seedlings to estimate the total number of new seedlings sampled in those years. While these conversions are rather arbitrary, they represent a more realistic portrayal of the density of new seedlings than if we had used only those seedlings less than 5 or 10 cm tall.

The 3-year trends in these estimated densities are portrayed for each treatment in Figure 22. The average densities of new Douglas-fir seedlings appear to be remarkably similar among all treatments when last surveyed in 1996, ranging from 11 033 to 15 689 stems/ha. Analyses of variance indicate no significant treatment effects on the density of new seedlings sampled in 1993, 1994, or 1996, nor over all years combined. Neither was there any significant difference among treatments in the ratio of 1994 germinant density to 1993 seed rain density, nor in the ratio of 1996 regeneration density to that sampled in 1993 (the first year with reliable density values). Trends indicate that the flush of new seedlings observed in 1994 was largely transitory, but the degree to which it persisted was greater in all 50% RBA units and the 70% RBA-FB units than in the uncut or 70% RBA-HF units.

3.9 Growth of Natural Regeneration

The advance regeneration of all species sampled in 1994 measured 26–98 cm tall, with an overall mean of 51.8 cm. Douglas-fir seedlings ranged in age from 8 to 36 years (mean of 19.3 years), and subalpine fir ranged from 13 to 27 years old (with a mean of 21 years); no hybrid white spruce ages were determined. Because seedlings varied so much in height at the time of logging, only relative height growth rates are presented in Table 13. Douglas-fir height growth from 1990 to 1994 ranged from an average relative growth rate of 0.35

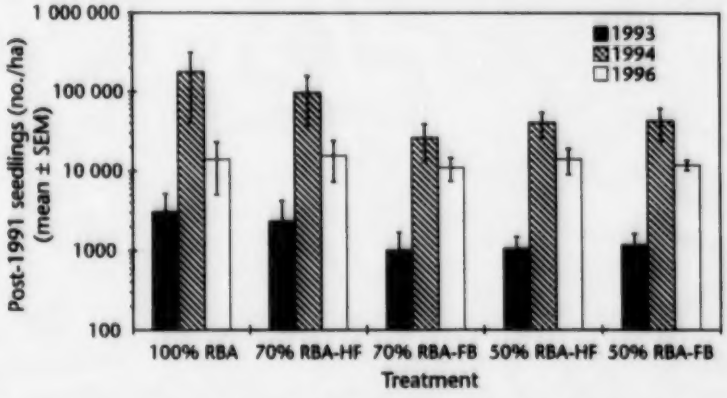

FIGURE 22 *Estimated densities of Douglas-fir seedlings likely to have germinated since harvesting in 1991, all locations combined.*

TABLE 13 *Retrospective growth analysis on natural regeneration conducted in 1994; mean ± S.E.M. and ANOVA results based on treatment unit means over all three locations*

Species	Attribute	Treatment*					ANOVA results	
		100% RBA	70% RBA-HF	70% RBA-FB	50% RBA-HF	50% RBA-FB	$F_{4,3}$	Prob. >F†
Douglas-fir	Number of seedlings measured	105	108	135	120	122		
	Relative height growth, $cm \cdot cm^{-1} \cdot yr^{-1}$	0.35±0.02	0.44±0.04	0.39±0.02	0.50±0.07	0.55±0.09	2.64	0.11
Hybrid white spruce	Number of seedlings measured	7	7	4	6	9		
	Relative height growth, $cm \cdot cm^{-1} \cdot yr^{-1}$	0.51±0.12	0.41±12	0.46±0.25	0.40±0.06	0.58±0.11	0.33	0.85
Subalpine fir	Number of seedlings measured	26	59	42	39	48		
	Relative height growth, $cm \cdot cm^{-1} \cdot yr^{-1}$	0.31±0.04	0.53±0.16	0.38±0.13	0.48±0.05	0.49±0.00	1.76	0.26

Note; Significant differences among treatments were tested for by analysis of variance (ANOVA).

* Treatments denoted by: RBA = residual basal area; HF = harvested by hand-falling; FB = harvested by feller-buncher.

† If Prob.<0.05 then the treatment effect is significant at the 95% confidence level.

$cm \cdot cm^{-1} \cdot yr^{-1}$ in control units to 0.55 $cm \cdot cm^{-1} \cdot yr^{-1}$ in 50% RBA-FB units. Hybrid white spruce also showed the best growth in 50% RBA-FB units (0.58 $cm \cdot cm^{-1} \cdot yr^{-1}$), while its poorest growth (0.40 $cm \cdot cm^{-1} \cdot yr^{-1}$) was found in 50% RBA-HF units (Table 13). The relative height growth of subalpine fir was lowest (0.31 $cm \cdot cm^{-1} \cdot yr^{-1}$) in control units, and highest in the 70% RBA-HF units (0.53 $cm \cdot cm^{-1} \cdot yr^{-1}$). Neither seedling sizes nor measurements of seedling growth in any species differed significantly among individual treatments at the $p = 0.05$ level (Table 13), though Douglas-fir growth was significantly greater in the two 50% RBA treatments than in both 70% RBA treatments ($F = 6.28$, $p = 0.037$).

3.10 Synthesis

3.10.1 Correlations and regression The summarized data on Douglas-fir regeneration used for correlation analysis are presented in Appendix 3 (Table A3.1). Pairwise correlations revealed some interesting trends in the relationship of regeneration variables to each other and to environmental conditions (Table 14). Because a total of 240 comparisons were made, a Bonferroni adjustment would suggest limiting interpretations of 95% significance to those correlations having a p value of 0.05/240 = 0.0002 or less.

As expected, relative irradiance was negatively correlated with stand basal area ($r = -0.78$, $p = 0.0001$, $n = 27$), and growing season heat sums were positively correlated with moisture stress integral (for some years, though not others). Surprisingly, overall seedfall was not significantly correlated with residual basal area.

Germination on any of the organic substrates (moss, forest floor, decayed wood) was negatively correlated ($r = -0.77$ to -0.83, $n = 6$) with growing season heat sums or moisture stress integral calculated for the 5 cm depth. Interestingly, germination on mineral soil did not show significant correlations to heat sums or moisture stress during the same growing season, but were negatively correlated with the degree of heat or moisture stress in the

TABLE 14 *Significant* results of correlation analysis among Douglas-fir regeneration variables and environmental attributes (data in Table A3.1); within each cell, values are r, p, and n, respectively*

		Environmental variables					Seed variables		Germination variables				Survival variables				Seedling variables	
Category	Variable	Relative† irradiance	Heat sums year n	Heat sums year n-1	Moist. stress 5cm, year n	Moist. stress 5cm, year n-1	Seedfall year n-1	Seed predation	Live moss	Forest floor	Decayed wood	Mineral soil	Live moss	Forest floor	Decayed wood	Mineral soil	Seedling density	Seed-to-seedling ratio
Environmental	Basal area	-0.7769 0.0001 27†	n.s.	n.s.	n.s.	n.s.	n.s.	-0.5494 0.0030 27	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.3431 0.080 27	0.2630 0.081 45	-0.3798 0.051 27
	Relative irradiance†	1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-0.5105 0.0065 27**	n.s.	n.s.	0.3788 0.051 27**	n.s.	n.s.
	Heat sums, year n		1	n.s.	n.s.	n.s.	0.7447 0.090 6	n.s.	n.s.	n.s.	-0.8295 0.041 6	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Heat sums year n-1			1	n.s.	0.7031 0.03 9	n.s.	n.s.	n.s.	n.s.	n.s.	-0.6254 0.072 9	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Moisture stress, year n				1	n.s.	n.s.	n.s.	-0.7720 0.072 6	-0.7723 0.072 6	-0.7941 0.059 6	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Moisture stress, year n-1					1	n.s.	n.s.	n.s.	n.s.	n.s.	-0.5886 0.096 9	n.s.	n.s.	-0.7081 0.032 9	n.s.	n.s.	n.s.
Seed	Seedfall year n-1						1	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.6921 0.0001 27	n.s.
	Seed predation							1	n.s.	n.s.	-0.4149 0.031 27	n.s.	n.s.	0.3804 0.055 27	0.4288 0.029 27	n.s.	n.s.	0.4230 0.028 27
Germination	Moss								1	0.7438 0.0001 27	0.7111 0.0001 27	0.7939 0.0001 27	0.3447 0.078 27	n.s.	n.s.	n.s.	n.s.	-0.3579 0.067 27
	Floor									1	0.6655 0.0002 27	0.8003 0.0001 27	n.s.	n.s.	n.s.	n.s.	0.4166 0.031 27	-0.4385 0.022 27
	Wood										1	0.4910 0.0093 27	n.s.	n.s.	n.s.	n.s.	n.s.	-0.3519 0.0719 27
	Soil											1	n.s.	0.3263 0.097 27	n.s.	n.s.	0.3266 0.096 27	-0.5474 0.0031 27
Survival	Moss												1	n.s.	0.4922 0.0091 27	n.s.	n.s.	n.s.
	Floor													1	0.3828 0.049 27	0.4452 0.020 27	n.s.	n.s.
	Wood														1	0.4465 0.020 27	n.s.	n.s.

Note: **Bold** numbers indicate statistically significant results.

* n.s. denotes $p > 0.10$; combinations not shown were also n.s.; because a total of 240 comparisons were made, a Bonferroni adjustment would suggest interpetting 95% significance only when $p \leq 0.0002$

† If limited to actual irradiance measurements (sampled only in 1993), then n = 9 and correlation with basal area is r = -0.071 (p = 0.030), correlation with germinant survival in live moss is r = -0.610 (p = 0.082), and correlation with germinant survival on mineral soil is not significant.

previous year. Germination levels were significantly correlated among all four seedbeds ($r = 0.49–0.80$, $n = 27$), suggesting an overriding importance of canopy treatment and/or year-to-year effects over those of substrate, as also indicated by analysis of variance (Section 3.6).

The survival of newly germinated Douglas-fir seedlings was negatively correlated with relative irradiance when growing in moss ($r = -0.51$, $p = 0.0065$, $n = 27$), but was positively correlated with irradiance when growing on mineral soil ($r = 0.38$, $p = 0.051$, $n = 27$). Germinant survival on decayed wood was negatively correlated ($r = -0.71$, $p = 0.032$, $n = 9$) with the amount of moisture stress experienced during the previous year. Survival on some seedbeds was positively correlated with germination and survival on other seedbeds, but these relationships were not very strong ($r < 0.35$).

The density of 1- to 2-year-old Douglas-fir germinants was marginally but positively correlated with the residual basal area of Douglas-fir in different treatment units ($r = 0.26$, $p = 0.0809$, $n = 45$). More pronounced, however, was the correlation of seedling density with the seed rain density observed in the previous year ($r = 0.69$, $p = 0.0001$, $n = 27$). Also noteworthy was the positive correlation ($r = 0.42$, $p = 0.031$, $n = 27$) of seedling density to the germination success observed on forest floor, the most abundant seedbed in all treatment units. Finally, seed-to-seedling ratios ($n = 27$) were negatively associated with basal area ($r = -0.38$, $p = 0.051$), germination capacity on all seedbed types ($r = -0.35$ to -0.55), and positively associated with levels of seed predation ($r = 0.42$, $p = 0.028$). This means that a larger proportion of seeds likely become seedlings in stands with high basal areas, less seed predator activity, and larger proportions of the more favourable seedbeds (such as mineral soil and decaying wood).

Multiple regression analysis was used to pick out the set of three variables most predictive of observed levels of regeneration density. The relationship with the best fit to the variables reported in Table A3.1 was density (stems/ha) = 5551.82566247 + 0.06172465 seedfall (seeds/ha) -13231.63542827 decayed wood cover (%) + 1741.00975614 moss mat germination (%); $r^2 = 0.6456$, $p = 0.0001$, $n = 27$. Even when analysis was restricted to those observations with complete heat sums and water stress data, those environmental variables were not as predictive as those more directly reflective of seed and seedling demography.

3.10.2 **Simulation** As described by the equation given in Section 2.12, empirical observations on seed germination and germinant survival from 1994 to 1996, applied to observed seedfall densities and seed predation rates, should be able to predict the observed densities of germinants measured in 1993, 1994, and 1996. Table A3.2 evaluates two measures of congruence in observed regeneration densities and the values estimated for the component processes responsible for successful natural regeneration. Table 15 provides another set of comparisons between model-predicted and observed Douglas-fir seedling densities, emphasizing the fact that all model variables are measured with error (and these errors can be multiplicative in a simulation model), and all seedling densities used for model verification are also sampled with some degree of error.

Chi-square analysis indicates that predicted and observed densities of seedlings are significantly different ($\text{chi-square}_{df=8} > 6000$ for each of the 3 years, whereas the critical chi-square for $p = 0.05$ and d.f. = 8 is 15.51). On average, predicted seedling densities were 58% less than observed densities,

TABLE 15 *Evaluation of model predictions, given the uncertainty in both the surveyed and modelled data*

Seedling Year	Treatment unit	Sampled germinant densities: lower 90% c.l.*	Sampled germinant densities: mean (per ha)	Sampled germinant densities: upper 90% c.l. (per ha)	Predicted germinant densities: lower 90% c.l. (per ha)	Predicted germinant densities: mean (per ha)	Predicted germinant densities: upper 90% c.l. (per ha)	Model performance: Predicted mean within obs. c.l.? (prediction is:)	Model performance: Sampled mean within predicted c.l.? (prediction is:)
1993	BC-50%RBA-FB	1015	1520	2025	119	3650	18 889	too high	in bounds
	BC-70%RBA-FB	1273	1747	2221	492	1989	5477	in bounds	in bounds
	BC-100%RBA	4696	6147	7598	396	2910	10 330	too low	in bounds
	GL-50%RBA-FB	286	453	620	6	204	1416	too low	in bounds
	GL-70%RBA-FB	30	120	210	0	4	18	too low	too low
	GL-100%RBA	670	1587	2504	1	310	2150	too low	in bounds
	UB-50%RBA-FB	376	760	1144	0	9	83	too low	too low
	UB-70%RBA-FB	54	293	532	0	86	456	in bounds	in bounds
	UB-100%RBA	18	120	222	0	96	651	in bounds	in bounds
1994	BC-50%RBA-FB	27 883	61 333	94 783	4073	34412	135 073	in bounds	in bounds
	BC-70%RBA-FB	7684	32 000	56 316	18 485	50 705	116 738	in bounds	in bounds
	BC-100%RBA	243 391	406 000	568 609	43 821	121 823	264 124	too low	too low
	GL-50%RBA-FB	6884	19 333	31 782	185	5726	28 623	too low	in bounds
	GL-70%RBA-FB	9244	19333	29422	87	940	2346	too low	too low
	GL-100%RBA	23 250	66 000	108 750	1201	17 039	71 530	too low	in bounds
	UB-50%RBA-FB	4488	11 333	18 178	0	2864	18 520	too low	in bounds
	UB-70%RBA-FB	0	2000	4550	19	2755	9956	in bounds	in bounds
	UB-100%RBA	0	8000	72 777	1	1623	10 027	in bounds	in bounds
1996	BC-50%RBA-FB	0	667	1842	79	1526	7246	in bounds	in bounds
	BC-70%RBA-FB	0	6667	14 288	1058	4933	14 310	in bounds	in bounds
	BC-100%RBA	0	10 667	21 733	237	3078	12 980	in bounds	in bounds
	GL-50%RBA-FB	902	6000	11 098	955	3462	11 054	in bounds	in bounds
	GL-70%RBA-FB	1288	4667	8046	0	599	2462	too low	too low
	GL-100%RBA	2235	6000	9765	77	1649	8140	too low	in bounds
	UB-50%RBA-FB	1608	6667	11 726	0	3181	13 614	in bounds	in bounds
	UB-70%RBA-FB	0	2000	4550	7	4308	21 234	in bounds	in bounds
	UB-100%RBA	0	1333	3680	174	1746	7221	in bounds	in bounds
(3 yrs)	50% RBA average	5089	12 007	18 982	591	5583	23 138	in bounds	in bounds
(3 yrs)	70% RBA average	3731	12 833	22 163	2362	9158	26 909	in bounds	in bounds
(3 yrs)	100% RBA average	28 389	50 132	78 341	4967	15 122	37 127	too low	too low
Overall average		12 492	25 287	40 332	2647	10 060	29 432	too low	in bounds

* c.l. = confidence limits

SUMMARY:		
model predictions too high:	1 (= 4%)	0
model predictions in bounds:	14 (= 52%)	22 (= 81%)
model predictions too low:	12 (= 44%)	5 (= 19%)

and underestimates were more prevalent than overestimates for individual treatment units in different years (Table A3.2). Predictions were less accurate in the control plots than in other treatment units, and less accurate in 1996 than in the other years. On the whole, however, there was good correlation between the predicted and observed seedling densities across all treatments and years ($r = 0.94$, $p = 0.0001$, $n = 27$) (Figure 23). This correlation of observed seedling densities with model-predicted densities is better than can be obtained with any individual factor (Tables 14 and A3.2), or by multiple regression.

The confidence intervals for surveyed seedling densities and for predicted seedling densities both tend to be very broad (Table 15). When comparing a fixed-mean model output with the 90% confidence limits for sampled seedling densities, 52% of the 27 treatment unit estimates are found to be in bounds. Conversely, the lower and upper 90% confidence limits for model predictions spanned the observed mean densities 81% of the time (Table 15). Most cases in which predicted and observed Douglas-fir seedling densities do not match are due to underestimates on the part of the model.

4 DISCUSSION

4.1 Seed Rain

Year-to-year variation in the seedfall density of all four species studied here (Table 2) is typical of the known seed biology of conifers (Eremko et al. 1989; Young and Young 1992; Leadem et al. 1997). Douglas-fir produced a large seed crop in 1993, with a medium seed crop in 1995 and practically no viable seed in 1997 (Figure 5). More unusual was the behaviour of hybrid white spruce, which supported good seed crops in 2 consecutive years, 1993 and 1994. Heavy seed production years for Douglas-fir seem to be associated with high

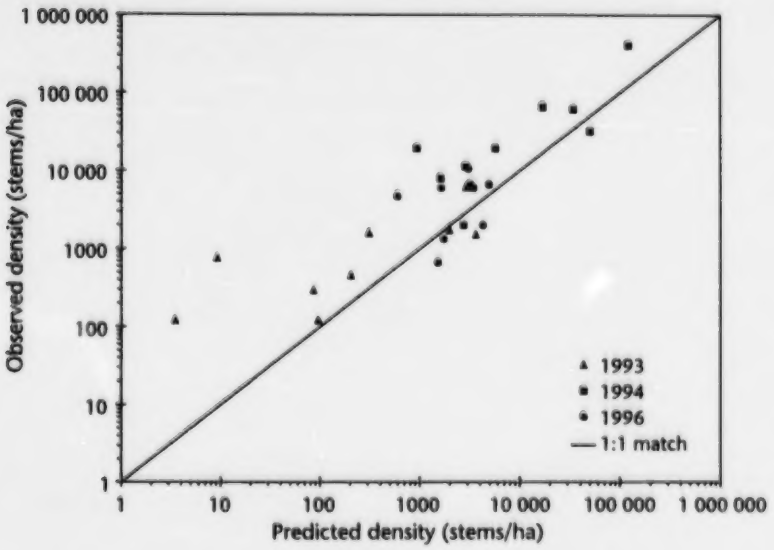

FIGURE 23 *Observed densities of Douglas-fir germinants in 1993, 1994, and 1996 compared to model predictions. Complete concurrence of observed and predicted densities is indicated by the 1:1 line.*

sunlight and high air temperature in the previous year, and relatively dry conditions during the year of seed dispersal (Table 3, Section 3.1).

These sub-boreal stands supported very high seed rain densities of Douglas-fir, with an average of more than 1.9 million sound seeds/ha estimated for 1993. The seed rain density of all conifer species over 6 years averaged 657 250 seeds·ha^{-1}·yr^{-1}, six times greater than the average conifer seed rain density (monitored over 5 years, and also including a heavy seed year) associated with successful regeneration in mixed-conifer shelterwoods located in eastern Oregon (Seidel et al. 1990). While control stands had the highest Douglas-fir seed rain in 1993 and 1994, the 50% RBA treatments induced a much greater seed crop in the medium crop-size year of 1995 (Table 2). This response had been expected to prevail in most years, because shelterwood cuttings in northern California have demonstrated 5–159% increases in Douglas-fir cone production, though this did not always translate to more viable seed on the ground (McDonald 1976; Roy 1979). It is generally agreed that increased canopy openness, greater exposure to sunlight, and incidental "girdling" associated with logging damage tends to stimulate the production of reproductive buds (Strothmann and Roy 1984; Leadem et al. 1997) but many countervailing factors can interfere before viable seeds are dispersed.

4.2 Seed Predation

Seed predation losses to small mammals also differed more from year to year and from month to month than among stand treatments. Seed losses in August, September, and October were generally higher in logged stands than in unlogged stands for the first few years after harvesting (Figure 9). These relatively small treatment units (1.4 ha each) may be too small to encompass the home ranges of most small mammals, and individuals likely foraged in more than one treatment unit.

Over all years, predation on Douglas-fir seeds (expressed as seed loss per day) was significantly greater in the harvested treatment units than in the uncut units. Red-backed vole (*Clethrionomys gapperi*) populations increased by three to four times from 1990 to 1991, especially in the partially cut stands (von Trebra et al. 1998). These small mammals may have been responsible for elevated seed predation losses in 1992 and 1993, but treatment differences in vole population densities were significant only in 1991 (von Trebra 1994). Deer mice (*Peromyscus maniculatus*) are considered more important seed eaters (Sullivan et al. 1990), but their population levels remained relatively constant (von Trebra et al. 1998).

Low predation rates reported for October and over winter may not be representative, because all years were not sampled over those periods. Seed predation losses appear to have dropped in mid-summer, then increased over late summer and early autumn (Figure 9). Von Trebra et al. (1998) attribute this trend to the seasonality of deer mouse and red-backed vole populations within these same stands, their numbers being higher in the fall. Daily losses to seed predators averaged 2.4–3.3% during the growing season, or 72–99% over a 30-day period. These rates are somewhat higher than other observations of seed losses to small mammals, which have been reported at rates of 70% in a 30-day period in another Douglas-fir seed loss study conducted in an Oregon clearcut (Gashwiler 1970).

4.3 Seedbed Distribution

Seedbeds were very much dominated by organic forest floor materials, even in the logged treatment units (Table 5, Figure 11). While it was expected that summer harvesting operations would expose large amounts of mineral soil,

it increased to an average of only 2% cover in the 50% RBA-FB units (Table 5). Logging operations were just as important in exposing well-rotted wood, from 2% cover in control blocks to 6% in most harvested units. The most significant change was the reduction of live moss cover, which dropped in direct proportion to the basal area of timber removed (Figure 11). It had been expected that higher forest floor disturbance would be found in the hand-falling treatment units because the trees were being felled onto the forest floor between trails, and then skidded across the ground surface, while the feller-buncher laid trees directly on the skid trail after cutting them. There was no support for this hypothesis, because the only significant planned contrast detected in the 1993 seedbed survey data was for mineral soil being more abundant in 50% RBA units than in 70% RBA units ($F_{1,8} = 16.72$, $p = 0.0035$).

Undecomposed coarse woody debris, logging slash, and other substrates unsuitable for seed germination occupy >42% of the ground area in logged blocks, compared to 30% of the ground area in control blocks. On balance, therefore, it could be argued that harvesting operations decreased the availability of suitable seedbeds. These slash and litter levels are higher than those reported for Scots pine (*Pinus sylvestris*) shelterwoods in southern Sweden (Béland et al. 1997) and are lower than those reported for mixed-conifer shelterwood cuttings in central Oregon (Seidel 1979). The net gain in suitable seedbeds, other than on skid trails, was much less than expected, and would benefit from augmentation through the use of mechanical scarification or prescribed burning. While there is little experience using controlled ground fire in sub-boreal Canadian forests, this practice (often termed "under-burning") is becoming more widely applied in midwestern oak-hickory forests (Brose and Van Lear 1997) and western mixed-conifer forests (Arno and Ottmar 1994) in the United States, and in southeastern British Columbia. On the other hand, high seedling densities in all treatments indicate that additional seedbed preparation is not necessary to achieve regeneration objectives.

4.4 Seed Germination

Germination of all four conifer species tested was highly sensitive to seedbed treatments, and all species showed the same rank order of seedbed preference, though the magnitude of differences varied. Rotting wood supported the most germination, followed by mineral soil, forest floor, and moss mats (Figure 13), the latter two sometimes being statistically indistinguishable. Fisher (1935) also reported that many conifers germinated best on rotting wood tested in a greenhouse trial. The preferential distribution of seedlings on rotting logs is a widespread phenomenon in western coniferous forests (Christy and Mack 1984).

Removal treatments had little effect on seed germination, though the 0% RBA (clearcut) treatment tested in 1996 allowed rotting wood and mineral soil to support higher levels of germination than under full or partial canopies (Figure 14). Though less pronounced for Douglas-fir germinating on rotting wood, this suggests that the shelterwood treatments did not sufficiently open the canopy to achieve optimal germination rates. Similar interactive substrate and canopy effects have also been inferred from observations on the establishment of hybrid white spruce and subalpine fir at Aleza Lake, B.C. (in the SBSwk1 biogeoclimatic variant) (Smith and Clark 1960).

It is clear that germination success is dependent on low moisture stress during the growing season, especially on organic seedbeds (Table 14).

A combination of warming and moisture retention appears to be critical to successful seed germination in the Sub-Boreal Spruce zone. Whereas germination of all four conifer species showed a significant positive correlation with relative irradiance when establishing on mineral soil (reflecting the beneficial effects of warming), they experienced a negative correlation with irradiance when establishing on moss mats, probably because of desiccation (Burton 1997). The need to protect seedbeds from high temperatures and high levels of evaporation is apparently greater in the Interior Douglas-fir zone and other forest types characterized by hotter, drier summers (Tesch and Mann 1991; Burton 1997). At these sites, and probably throughout the Sub-Boreal Spruce zone, seedbed warming tends to be more important to conifer germination than the risk of seedbed desiccation.

4.5 Germinant Survival

The survival of newly germinated seedlings was relatively constant across species and treatments. Survival of all four species tested was equally superior (>54% over one growing season) on rotting wood and mineral soil (Figure 16). Douglas-fir and subalpine fir also survived equally well on a forest floor substrate. Minore (1972) observed similar behaviour in Douglas-fir germination and early survival, as long as the duff material was well watered.

Survival of hybrid white spruce and lodgepole pine was intermediate on forest floor, while moss was universally inferior in supporting germinant survival of all species. Greene and Johnson (1998) likewise report moss to be the worst possible seedbed for supporting early conifer survivorship. Only subalpine fir, and this only in 1996, showed significant responses to canopy removal treatments. This species survived more poorly in fully open conditions, suggesting that it needs a degree of protection for establishment in this climate. In more coastal biogeoclimatic zones (having more cloud cover), canopy effects on germinant survival are often more pronounced, with open conditions being more favourable than shaded conditions (Burton 1997).

Mineral soil under the 50% and 0% RBA treatments supported the best overall Douglas-fir survival, while moss mats in the same treatment units had the poorest survival. Correlation analysis (Table 14) further confirmed that Douglas-fir germinant survival on mineral soil was positively related to available light, whereas survival on moss mats was negatively related to irradiance (presumably because the moss dries out in direct sunlight). This suggests that higher levels of light availability are desirable for encouraging Douglas-fir regeneration, but they must be accompanied by site scarification techniques in order to disrupt the widespread moss cover and expose the more desirable mineral soil and rotting wood seedbeds. Similar conclusions have been reached for the use of shelterwood reproduction methods in southwestern Oregon (Tesch and Mann 1991). Conversely, if understory scarification cannot be conducted, one may wish to retain approximately 70% residual basal area in order for forest floor and moss materials to sustain the best Douglas-fir germinant survival possible for those seedbeds.

4.6 Regeneration Densities

Through the chance allocation of treatments among experimental units, large spruce regeneration ranged in estimated densities from 247 to 910 stems/ha among units slated for different treatments (Table A2.1, Table 7). No other species or size classes of regeneration exhibited significant differences among treatment categories prior to harvesting. Following logging activities in 1991, no significant treatment differences in regeneration density class distribution were found (Table 9, Table A2.2).

No treatment differences had emerged by 1993 either (Table 10), though regeneration densities had exhibited a general increase (across all species and size classes) from the levels estimated for 1991. No species of regeneration exhibited significantly greater density in any particular treatment in 1993 or 1994. However, mean densities of all species of regeneration in 1994 ranged from three to 11 times those found in 1993, reflecting the substantial input of seeds during the autumn of 1993. The density of Douglas-fir germinants was especially high in treatment units having the greatest density of overstory trees (the 100% RBA units and the 70% RBA-FB units), though variability was too great to result in significant treatment differences (Table 11). No substantial treatment differences were found in 1996 either (Table 12). Regeneration densities in 1996 were less than those found in 1994 (because many of the 1994 germinants had presumably died in the interim), but were still greater than mean 1993 densities. Interestingly, the density of all sizes of all species returned almost exactly to 1993 levels (just over 17 000 stems/ha) in the uncut units, while partially cut units still supported 23–79% more seedlings than they did in 1993.

In 1994, 3 years after partial cutting, harvested stands supported mean Douglas-fir regeneration densities ranging from 38 791 to 102 436 stems/ha (Table 12). These densities compare well with those obtained in Douglas-fir shelterwoods elsewhere. A similar response was obtained under a partial cutting trial in a mixed-conifer forest in Oregon, in which Douglas-fir regeneration jumped from 14 678 to 36 282 stems/ha on scarified seedbeds 3 years after logging, and from 2735 to 4589 stems/ha on unscarified seedbeds (Minore et al. 1977). Five years after harvesting, the density of all species and sizes of regeneration in our experiment supported average densities of 16 698 to 19,547 stems/ha (Table 12). In contrast, another shelterwood trial conducted in eastern Oregon supported more than 49 000 seedlings per ha 5 years after harvesting, even with livestock grazing in the stand (Seidel et al. 1990).

The density of small Douglas-fir seedlings and germinants was positively correlated with stand basal area, seedfall density from the previous autumn, and germination rates on forest floor and mineral soil seedbeds (Table 14). Stepwise multiple regression likewise selected seedfall, the cover of rotting wood, and germination rates in moss as being most useful in predicting the density of new Douglas-fir seedlings. Collectively, these relationships indicate the importance of seed inputs and germination on duff in explaining the overall abundance of natural regeneration.

Why are treatment effects not more pronounced 5 years after harvesting? The answer is largely that increases in seed (and hence seedling) density are associated with greater residual basal areas and overstory tree densities, whereas growth and survival of seedlings are generally associated with more open conditions. Subcanopy light measurements (Table 3) indicate that post-harvesting light levels in the 70% and 50% RBA treatments are statistically indistinct, and averaged only 13–23% of full sunlight. Retrospective measurements of conifer seedling height growth (Table 13) have detected marginally significant differences in Douglas-fir growth under more open conditions. This suggests that subcanopy conditions may not yet be open enough to enhance the early growth and survival of conifer seedlings; improvements can be expected after the second entry in the 70% RBA treatment units. The canopy retention threshold necessary for preventing frosts, while still promoting seedling growth and survival, remains to be determined.

Microclimate data (Table 3) clearly indicate that killing frosts common in clearcuts in the study area can be avoided under both of the shelterwood canopies tested. However, we do not yet know how low a residual basal area can simultaneously achieve high levels of regeneration and protection from frosts.

4.7 Synthesis

Effective natural regeneration depends on an adequate seed supply, a suitable seedbed, and an appropriate set of environmental conditions (Roe et al. 1970). Each of these three general factors is a necessary, but not in itself sufficient, requirement for successful natural regeneration, and each has a number of contributing components. Since regeneration in this shelterwood trial peaked in 1994 and then declined in 1996, it remains to be seen whether or not we have the appropriate data to explain the densities of Douglas-fir (or other) seedlings, and their dynamics, observed to date. Other researchers have used statistical associations with site and treatment factors in order to predict the species composition and density of natural regeneration on the basis of elevation, slope and aspect, time since disturbance, etc. (Ferguson et al. 1986). The framework for an alternative mechanistic model is presented in Figure 2, in which influential factors act successively to decrease the density of viable Douglas-fir seeds and seedlings.

Does such a model improve our understanding or predictive ability when it comes to explaining observed patterns of natural regeneration? Have we documented and measured all the relevant components of a successful natural regeneration program? The answer to both questions is "yes," to the extent that better correlations between predicted and observed seedling densities can be achieved than through simple correlation with any single factor. Using the values presented in Table A3.2, model predictions generate a correlation with observed seedling densities of $r = 0.94$, whereas the highest raw correlation (with seedfall density the year before) was only $r = 0.70$.

It could be argued that the absolute values of predicted seedling densities are still too far removed from observed seedling densities (as demonstrated by a significant chi-square result) to be used for predictive purposes. However, it is important to remember that discussion or portrayal of simple mean densities (e.g., as in Figure 23) ignores the uncertainty inherent in estimating seedling densities and in estimating any variable used to model these densities. In fact, 22 of the 27 points (predicted treatment unit density estimates) portrayed in Figure 23 have 90% confidence limits that overlap the 1:1 line denoting perfect prediction (as detailed in Table 15). In conclusion, it is likely that improving our ability to predict natural regeneration densities depends more on enhancing the precision of our estimates of seedling densities, and the known factors that influence them (through increased sampling), than on the inclusion of additional variables in a natural regeneration model.

4.8 Management Implications

As of 5 years after harvesting, no particular treatment has emerged as superior for encouraging natural regeneration in these stands dominated by even-aged interior Douglas-fir. Yet many of the results and trends exhibited in this trial to date provide useful guidance for the regeneration of Douglas-fir in the SBSdw subzone.

First, it is clear that the retention of even 50% residual basal area effectively reduces the incidence of ground-level frosts during the growing season (Table 3). Secondly, all partial cutting treatments generated densities of new

Douglas-fir seedlings (likely to have established since 1991) of more than 1530 stems/ha in each such unit by 1996, and most logged units had much higher densities, up to 30 433 stems/ha. These stands will likely be considered fully stocked, depending on how well dispersed these seedlings are after the removal of the overwood (a procedure that should serve to thin out some of the new regeneration). Thus all four combinations of residual basal area and harvesting method can be considered effective in achieving the forest regeneration goals for implementing shelterwood treatments in these forests.

Suitable seedbeds to support optimal conifer germination covered only 0.8–11.9% of the surface area of treatment units surveyed 2 years after logging. Mineral soil exposure was significantly greater in the more heavily logged units, but showed no response to the method of logging, and covered less than 5% of any treatment unit. Much more prevalent was the exposure of rotting wood (up to 10.9% cover), which was found to support germination and germinant survival equal to or better than that observed on mineral soil. While the heavy seed crop of 1993 minimized seedbed limitations in this particular trial, the poor germination and germinant survival rates observed on forest floor and moss suggest that seedbed preparation must remain a consideration when prescribing shelterwoods designed to encourage natural regeneration of Douglas-fir in the Sub-Boreal Spruce zone. The more widespread machine activity associated with harvesting a larger proportion of the original basal area can increase the exposure of mineral soil somewhat. Other options include the use of mechanical scarification (Tesch and Mann 1991; Béland et al. 1997) or prescribed fire (Arno and Ottmar 1994; Brose and Van Lear 1997) soon after the seed cut. More important in the long run may be the need to implement practices to assure the future generation of coarse woody debris as a source of rotting wood seedbeds and a number of other roles in ecosystem processes (Caza 1993).

Suitable levels of seed production, seedling emergence, and frost protection were achieved in all four treatments, so a wide degree of latitude exists when implementing shelterwood prescriptions in these mixed Douglas-fir / lodgepole pine forests in the SBSdw subzone. There is a slight advantage for seedling survival (at least for those growing on mineral soil) and growth if they receive higher levels of sunlight, suggesting that the 50% RBA treatment is more appropriate than the 70% RBA treatment in promoting crop development. Logging by feller-buncher may have left more advance regeneration undamaged, though logging method had no significant effect on the density of new seedlings. Based on the results and trends observed to date, we consider the 50% RBA-FB procedure as the most effective treatment tested so far.

There seems little need, from a perspective of forest regeneration, to implement a three-pass shelterwood with a 70% RBA preparatory cut in this forest type. Therefore, it is advisable for the future application of shelterwoods in this subzone to be implemented according to a two-stage plan, leaving 50% RBA or less in the seed cut. It remains to be determined if less than 50% RBA could still achieve regeneration and frost protection goals. Other considerations not evaluated in this report (such as economic efficiencies, access planning, windthrow, wildlife habitat suitability, and visual quality issues) may additionally weight the selection of alternative or novel shelterwood treatments.

4.9 Suggestions for Further Study

The findings obtained to date also have some implications to the ongoing management of this trial, and to the design and implementation of similar

experiments. When the seed cut of the three-stage (70% RBA) treatment is conducted in 2001, it would be wise to log by feller-buncher in the winter in order to provide maximum protection to the considerable densities of advance regeneration already in the understory. Thinning the overstory to approximately 33% RBA (20 m^2/ha) would greatly increase understory light levels and conifer growth potential, as long as canopy gaps are not made so large as to significantly increase the sky view factor (which could lead to more radiation frost). Surveys of seedbed cover and regeneration densities should once again be conducted before and after logging. It would be a good idea to unobtrusively tag all existing seedlings in permanent sample plots prior to logging (e.g., with a loop of coloured wire around the base of each seedling) so that new and pre-existing seedlings can be clearly distinguished in the years following the seed cut.

While this experiment's design of having all treatments replicated at three separate locations facilitates a valid analysis of variance, other aspects of the current design still limit full interpretation of some results. Open conditions were evaluated in microclimate and germination monitoring, but a clearcut (0% RBA) treatment was not part of the overall experimental design. This experiment would not have been implemented if clearcutting had been successful in promoting Douglas-fir regeneration in the SBSdw1 variant. However, it is often useful to include extremes (such as 100% RBA and 0% RBA), even when neither is a practical management option, when evaluating a range of treatments. Such comparisons facilitate the interpretation and demonstration of treatment results.

The early (1990 and 1991) use of regeneration density classes and substrate cover classes makes an accurate assessment of differences among treatments or years difficult and unreliable. Actual density counts and percent cover estimates are superior because they allow the detection of slight, but quantitatively significant, differences between treatments or over time. Data collected in 1994 and 1996 are superior for being partitioned into five size classes, but their origin from three different plot sizes, nested within each other, may be problematic. Due to the clustered nature of natural regeneration, small plot sizes, especially those 1.0 m^2 in area, are rather "hit or miss" in their ability to include a representative count of seedlings. This clustering means that the resulting density counts are highly variable from point to point, and suggests that a single, larger plot size (e.g., 50 m^2), would be more appropriate for all sizes of regeneration. Alternatively, an equivalent total sample area in many small plots used to sample the smaller seedlings may be appropriate. For example, if a very high density of seedlings (as encountered in 1994) makes sampling too laborious, then multiple subsamples (e.g., three small plots each measuring 1.0 m^2) could be randomly located within the larger plot. Efforts to correlate germinant densities with seedbed coverage would be facilitated by counting germinants and estimating percent substrate cover in the same small (1.0 m^2) plot. Future monitoring should use the same five regeneration size classes as used in 1994 and 1996.

If a similar silvicultural trial is established in the future, an experimental design similar to that employed in this project (replicated at three or more locations) can be highly recommended. It should further incorporate larger treatment units (e.g., at least 5 ha each), a very heavy removal treatment (leaving, for example, only 30% residual basal area), as well as extreme treatments of 0% RBA and 100% RBA. Though we did not emphasize their interpretation within the experimental design employed here, site-to-site

differences can be quite pronounced even within the same biogeoclimatic subzone and geographic vicinity. Such differences illustrate the importance of site-specific evaluation when testing relatively new silvicultural systems in a given forest type.

5 CONCLUSIONS

This silvicultural systems trial, with measurements initiated in 1990, provided an opportunity to investigate many of the component mechanisms responsible for the successful natural regeneration of interior Douglas-fir in the SBSdw1 variant after partial cutting. Seed rain density varied considerably from year to year, with Douglas-fir producing outstanding or good seed crops in 1993 and 1995, and hybrid white spruce producing good seed crops in 1993 and 1994. There were marginally more Douglas-fir seeds produced in the 50% RBA treatment units than in the control stands in 1995, as found in comparable studies in the western United States, but this trend was not found in other years. While further seedfall monitoring and a greater sampling effort might eventually identify significant treatment differences, it appears that treatment differences in seed rain are much less important than stand-to-stand (location) and year-to-year differences. This means that a single value to describe mean seedfall density, with confidence limits, can be used to describe the seed rain under a wide range of residual basal areas in a given year. It is very difficult to predict seed production in any given year, though good seed crops seem conditional on warm, sunny weather and light seed production the year before, and a period of drought in the current growing season.

Seed predation levels also varied considerably from year to year, partially reflecting a 3- to 4-year cycle of vole abundance (von Trebra et al. 1998). Seed losses were significantly greater in the partially cut treatment units. In general, losses to seed predators averaged 2.4–3.3% per day during the growing season. Seed losses increased in the partially cut treatment units from July to September, but stayed relatively constant in the uncut control stands. Integrated across entire growing seasons, these rates of seed consumption under shelterwood treatments translate to total losses ranging from 70.8–99.6% of all seeds that reach the ground.

Timber harvesting disrupted the organic materials constituting most of the ground cover in these forests. Though mineral soil exposure was increased from 0.4% cover in undisturbed stands to 2.2% cover in 50% RBA treatment units, rotten wood was more abundant throughout the study area and was increased from an average of 2.0% cover in uncut stands to 5.9% across all of the harvested units. The cover of live moss was also sensitive to disruption, in direct proportion to the degree of basal area removal. Disturbed substrates still covered an average of only 7.3% (maximum of 12%) of the understory in all of the partially logged treatment units, primarily on skid trails. Conifer germination levels on forest floor seedbeds are generally low (<20%) in these forests, and 40–80% of these seedlings are likely to die during their first growing season (Burton 1997). These results suggest that additional scarification may be beneficial to seed germination and early seedling establishment.

Despite high levels of seed predation and the sparse cover of favourable seedbed materials, sufficient Douglas-fir seeds were produced in 1993 that many managed to escape predation. Then the weather conditions in the spring of 1994 were sufficiently favourable for germination so that a noticeable flush of new seedlings was evident later that summer. Such cohorts of germinants are usually ephemeral, and most of them had died by the time plots were re-sampled in 1996. Their density in the uncut units returned to pre-1994 levels, but persisted at elevated levels in all partially cut treatment units.

No significant differences among the four alternative treatments, nor any difference from an uncut control, were observed in the density of natural regeneration during the first 5 years after the establishment of this trial. Implementation of the seed cut in the three-step shelterwood treatment (currently having 70% residual basal area), and continued monitoring of all treatments, is needed in order to evaluate these treatments further. Though the 70% RBA-HF treatment supported the greatest average density of Douglas-fir regeneration when sampled in 1996, this density was not significantly greater than that observed under other treatments. There are several indications that lower residual basal areas and harvesting by feller-buncher are more favourable for the survival and growth of Douglas-fir seedlings.

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APPENDIX 1 Partitioning of variance associated with germination and germinant survival

TABLE A1.1 *Partitioning of variance and significance of substrate and removal effects on seed germination*

Species	Year	Substrate treatment*			Canopy treatment†			Substrate x canopy		
		$F_{3,6}$	Prob.>F	% Var.	$F_{2,4}$	Prob.>F	% Var.	$F_{6,12}$	Prob.>F	% Var.
Douglas-fir	1994	9.94	**0.0096**	19.6	0.49	0.64	1.1	1.41	0.29	2.4
	1995	15.12	**0.0033**	21.6	2.11	0.24	4.0	0.85	0.57	2.3
	1996	17.16	**0.0024**	30.9	0.88	0.50	4.0	0.85	0.57	2.3
	all years	25.13	**0.0009**	19.7	1.45	0.32	2.8	2.74	**0.033**	3.4
Hybrid white spruce	1994	9.58	**0.011**	26.2	0.37	0.71	0.9	0.88	0.54	1.9
	1995	9.46	**0.011**	46.7	1.07	0.42	1.3	0.29	0.93	0.5
	1996	26.17	**0.0008**	49.5	0.95	0.47	2.2	3.02	**0.022**	6.2
	all years	31.28	**0.0005**	34.0	0.96	0.47	1.5	2.20	0.074	2.7
Lodgepole pine	1994	11.04	**0.0074**	25.8	0.14	0.87	0.8	0.69	0.66	2.1
	1995	8.97	**0.012**	35.4	2.31	0.22	2.1	0.60	0.72	1.5
	1996	23.42	**0.0010**	38.1	2.72	0.14	6.3	2.81	**0.030**	7.2
	all years	22.59	**0.0011**	25.6	1.87	0.24	3.6	2.59	**0.041**	3.4
Subalpine fir	1995	20.76	**0.0014**	37.3	1.96	0.26	1.6	3.18	**0.042**	3.0
	1996	16.53	**0.0026**	33.1	0.48	0.71	1.2	5.68	**0.0009**	12.9
	both years	22.45	**0.0012**	16.0	0.32	0.81	0.4	6.58	**0.0004**	5.6

Note: **Bold** numbers indicate statistically significant results.

* Substrate treatments consist of live moss mats, forest floor, rotting wood, and mineral soil.

† Three canopy opening treatments (leaving 100%, 70%, and 50% residual basal area) in 1994 and 1995, with a fourth treatment (having 0% residual basal area) added in 1996, make $F_{3,6}$ the appropriate statistic for testing canopy effects, and $F_{9,18}$ for substrate × canopy effects in 1996 and all years combined.

TABLE A1.2 *Partitioning of variance and significance of substrate and removal effects on the first-year survival of newly germinated tree seedlings*

		Substrate treatment*			Canopy treatment†			Substrate x canopy		
Species	Year	$F_{3,6}$	Prob.>F	% Var.	$F_{2,4}$	Prob.>F	% Var.	$F_{6,12}$	Prob.>F	% Var.
Douglas-fir	1994	3.29	0.100	3.3	0.51	0.63	3.1	0.29	0.93	1.8
	1995	2.09	0.20	5.3	1.88	0.30	7.4	2.61	0.12	10.3
	1996	5.17	**0.042**	9.1	1.62	0.28	6.7	2.91	**0.028**	9.1
	all years	3.44	0.092	4.9	1.51	0.31	4.1	2.79	**0.031**	4.1
Hybrid white spruce	1994	3.07	0.11	8.9	3.74	0.12	4.9	0.52	0.79	5.7
	1995	3.65	0.12	8.3	0.30	0.75	1.3	0.41	0.79	1.6
	1996	17.97	**0.0021**	18.5	0.88	0.50	2.6	0.87	0.57	5.2
	all years	9.34	**0.011**	6.5	1.63	0.28	1.8	0.63	0.76	2.9
Lodgepole pine	1994	2.01	0.20	6.5	3.03	0.16	3.9	2.95	0.071	7.2
	1995	0.98	0.47	3.3	0.74	0.53	3.1	0.79	0.60	2.9
	1996	31.50	**0.0005**	21.3	1.08	0.43	1.6	0.98	0.49	5.4
	all years	10.07	**0.0093**	8.6	0.93	0.48	1.1	0.83	0.60	2.9
Subalpine fir	1995	1.00	0.46	4.6	3.73	0.12	3.2	0.37	0.88	3.7
	1996	27.81	**0.0006**	20.5	6.33	**0.027**	12.5	1.28	0.31	4.7
	both years	6.57	**0.025**	6.6	7.92	**0.017**	8.4	0.65	0.74	2.4

Note: **Bold** numbers indicate statistically significant results.

* Substrate treatments consist of live moss mats, forest floor, rotting wood, and mineral soil.

† Three canopy opening treatments (leaving 100%, 70%, and 50% residual basal area) in 1994 and 1995, with a fourth treatment (having 0% residual basal area) added in 1996, make $F_{3,6}$ the appropriate statistic for testing canopy effects, and $F_{9,18}$ for substrate × canopy effects in 1996 and all years combined.

TABLE A2.1 *Regeneration densities (mean stems per ha, ± S.E.M.) in 1990, estimated* from density classes (Table 6), comparing treatments across all three locations*

Species	Size class†	Treatment					ANOVA results	
		100%	70%-HF	70%-FB	50%-HF	50%-FB	$F_{4,8}$	Prob.>F‡
Douglas-fir	small	4734±2729	5444±3992	4383±2988	3539±1536	3829±333	0.48	0.75
	large	5634±3166	5628±2824	7387±2792	6440±1932	7417±2263	1.54	0.28
	poles	36±24	18±9	728±653	18±9	442±429	0.99	0.47
	all	10 403±5887	11 090±6701	12 498±6429	9996±3459	11 688±2869	0.96	0.48
Hybrid white spruce	small	9±9	18±18	69±45	27±0	51±51	0.52	0.73
	large	247±91	464±183	580±242	624±454	910±561	4.27	**0.039**
	poles	96±71	227±123	338±170	62±24	424±308	1.51	0.29
	all	351±155	709±279	987±429	712±476	1386±919	3.28	0.072
Lodgepole pine	small	0	9±9	0	0	0	1.00	0.46
	large	0	9±9	0	0	0	1.00	0.46
	poles	0	0	0	0	0	-	-
	all	0	18±18	0	0	0	1.00	0.46
Subalpine fir	small	0	18±18	0	0	264±264	1.00	0.46
	large	420±46	980±584	1421±434	561±126	848±203	0.80	0.56
	poles	149±75	418±175	1446±447	185±104	222±133	3.16	0.078
	all	569±61	1416±756	2467±576	745±204	1334±491	0.93	0.49
All species combined	small	4743±2729	5488±4013	4452±3033	3829±1642	3880±359	0.49	0.74
	large	6300±3281	7082±2218	9388±2609	7911±2217	9103±2565	2.13	0.17
	poles	280±127	671±288	2512±805	311±117	1202±842	2.08	0.18
	all	11 323±6083	13 241±5918	16 352±6275	12 052±3744	14 185±3613	1.51	0.29

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed densities followed by Scheffé's multiple comparison tests, none of which showed significant differences among treatments at the p = 0.05 confidence level. **Bold** numbers indicate statistically significant results.

* Densities estimated by assigning the midpoint of the density classes described in Section 2.7: 0 = 0 sph; 1 = 400 sph; 2 = 1100 sph; 3 = 2700 sph; 4 = 5900 sph; 5 = 11 460 sph.

† Size classes: small = ≤5.0 cm tall; large = 5.1–100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

‡ If Prob. <0.05 then the treatment effect is significant at the 95% level of confidence.

TABLE A2.2 *Regeneration densities (mean stems per ha, ± S.E.M.) in 1991, estimated* from density classes (Table 8), comparing treatments across all three locations*

Species	Size class†	Treatment					ANOVA results	
		100%	70%-HF	70%-FB	50%-HF	50%-FB	$F_{4,8}$	Prob.>F‡
Douglas-fir	small	2736±1721	1430±1038	1215±875	877±433	1122±499	1.46	0.30
	large	5529±3190	3168±1924	5549±2858	4066±1567	4257±2127	0.59	0.68
	poles	44±18	0	9±9	0	0	4.27	**0.039**
	all	8310±4923	4598±2962	6773±3729	4943±2000	5379±2626	0.41	0.80
Hybrid white spruce	small	9±9	33±33	36±36	18±9	53±53	0.74	0.59
	large	291±82 b	267±137 b	602±240 a	387±190 ab	678±385 a	4.55	**0.033**
	poles	9±9	0	9±9	0	18±9	1.00	0.46
	all	309±88 b	300±170 b	647±267 ab	404±195 ab	749±442 a	4.20	**0.040**
Lodgepole pine	small	0	0	0	0	0	-	-
	large	0	0	0	0	0	-	-
	poles	0	0	0	0	0	-	-
	all	0	0	0	0	0	-	-
Subalpine fir	small	9±9	9±9	0	9±9	0	0.40	0.80
	large	631±121	1118±537	1799±225	516±289	671±72	1.39	0.32
	poles	0.00	0	0	0	9±9	1.00	0.46
	all	640±129	1127±544	1799±225	524±287	680±69	1.22	0.37
All species combined	small	2754±1738	1472±1065	1250±910	904±433	1176±552	1.41	0.31
	large	6451±3380	4552±1544	7951±3007	4968±1439	5606±2454	1.22	0.38
	poles	53±15	0	18±18	0	27±15	2.88	0.095
	all	9259±5123	6024±2605	9219±3911	5872±1870	6808±3008	0.83	0.54

Note: Significant differences among treatments were determined by analysis of variance (ANOVA) on log-transformed densities followed by Scheffé's multiple comparison tests, none of which showed significant differences among treatments at the p = 0.05 confidence level. **Bold** numbers indicate statistically significant results.

* Densities estimated by assigning the midpoint of the density classes described in Section 2.7: 0 = 0 sph; 1 = 400 sph; 2 = 1100 sph; 3 = 2700 sph; 4 = 5900 sph; 5 = 11 460 sph.

† Size classes: small = ≤5.0 cm tall; large = 5.1–100 cm tall; poles = 101 cm tall to 7.5 cm dbh.

‡ If Prob. <0.05 then the treatment effect is significant at the 95% level of confidence.

APPENDIX 3 Summarized Douglas-fir regeneration and environmental data used in correlation and simulation modelling

TABLE A3.1 *Regeneration and environmental values used for correlation and multiple regression analysis, Douglas-fir, 1993, 1994, and 1996*

Seedling year (n)	Treatment unit	Basal area year n-2	Rel.irrad. % full	Heat sum year n	Heat sum year n-1	WSI -5cm year n	WSI -5cm year n-1	Seedfall year n-1	% Seed predation	Seed germination %				Germinant survival %				Germinant density
										LM	FF	DW	MS	LM	FF	DW	MS	
1993	BC-50%RBA-FB	20.90	20.76	1067	1170	1314	1030	275676	85.15	20.4	12.2	60.7	43.1	36.7	80.2	75.9	88.2	1520
	BC-50%RBA-HF	30.66																1120
	BC-70%RBA-FB	30.11	16.24	1015	1273	415	1426	91892	89.20	36.9	53.4	76.7	56.7	51.4	81.6	79.0	55.8	1747
	BC-70%RBA-HF	35.90																5507
	BC-100%RBA	50.56	10.70	1016	1155	945	1299	118919	81.71	22.2	53.0	76.4	57.3	50.6	61.7	72.9	50.9	6147
	GL-50%RBA-FB	22.52	16.40					43243	81.28	5.3	0.8	47.7	11.7	38.6	33.3	68.3	75.6	453
	GL-50%RBA-HF	33.13																987
	GL-70%RBA-FB	37.81	8.74					48649	99.58	2.9	2.4	15.8	25.4	63.9	67.9	79.1	65.2	120
	GL-70%RBA-HF	37.82																760
	GL-100%RBA	57.52	3.11					32432	74.58	12.0	6.0	43.3	27.4	58.7	70.7	73.3	70.1	1587
	UB-50%RBA-FB	28.58	29.97					10811	91.12	0.9	1.1	43.0	24.0	12.5	66.7	66.9	76.0	760
	UB-50%RBA-HF	29.86																213
	UB-70%RBA-FB	24.97	15.13					78378	94.11	1.8	3.3	49.8	10.1	55.6	76.6	68.4	69.5	293
	UB-70%RBA-HF	29.23																13
	UB-100%RBA	39.55	5.80					24324	82.15	9.6	8.8	62.1	16.6	25.6	31.9	30.0	41.7	120
1994	BC-50%RBA-FB	20.70	20.56	1252	1067	1299	1314	2759459	85.96	15.0	19.3	42.3	56.3	54.0	77.7	67.9	89.5	61333
	BC-50%RBA-HF	29.74																44667
	BC-70%RBA-FB	29.98	16.24	1111	1015	590	415	2602703	89.60	21.0	66.3	77.7	76.0	50.5	83.8	84.0	79.2	32000
	BC-70%RBA-HF	35.82																186000
	BC-100%RBA	48.29	10.70	1116	1016	985	945	3524324	76.85	24.3	63.3	68.0	60.3	49.7	65.8	70.2	37.4	406000
	GL-50%RBA-FB	21.68	20.11					1289189	77.77	5.3	0.7	43.7	24.3	39.1	0.0	63.2	48.9	19333
	GL-50%RBA-HF	32.48																41333
	GL-70%RBA-FB	37.81	8.74					1554054	96.76	2.3	3.7	12.0	31.3	33.3	75.0	66.0	46.0	19333
	GL-70%RBA-HF	37.29																51333
	GL-100%RBA	57.25	3.70					1762162	74.72	18.3	1.0	39.0	48.0	71.5	100.0	61.9	75.4	66000
	UB-50%RBA-FB	28.32	29.97					1359459	83.04	1.0	0.7	37.3	41.3	0.1	100.0	42.0	78.3	11333
	UB-50%RBA-HF	29.51																6667
	UB-70%RBA-FB	24.71	18.71					1113514	86.70	1.3	2.0	9.7	7.7	50.0	75.0	80.0	65.0	2000
	UB-70%RBA-HF	28.95																10667
	UB-100%RBA	39.42	11.93					1354054	70.83	4.3	1.0	45.7	3.7	6.7	0.0	26.7	46.7	8000
1996	BC-50%RBA-FB	20.30	20.76		1127		753	198198	90.28	36.7	3.3	73.3	49.3	33.5	90.0	69.7	92.3	667
	BC-50%RBA-HF	27.99																4667
	BC-70%RBA-FB	29.72	16.40		1020		161	189189	88.00	43.0	55.0	70.7	66.7	65.8	85.9	88.1	58.2	6667
	BC-70%RBA-HF	35.66																20000
	BC-100%RBA	43.83	10.70		1039		286	89189	82.02	38.3	57.7	83.7	65.7	69.2	57.6	83.2	67.9	10667
	GL-50%RBA-FB	19.93	20.92					945946	89.47	2.0	0.7	51.2	4.3	25.0	100.0	97.7	97.9	6000
	GL-50%RBA-HF	31.27																13333
	GL-70%RBA-FB	37.81	8.74					772973	96.22	4.0	1.0	22.3	28.0	94.4	66.7	95.5	69.1	4667
	GL-70%RBA-HF	36.33																6667
	GL-100%RBA	56.72	3.95					418919	76.63	5.0	2.0	52.0	29.3	35.7	66.7	88.3	85.1	6000
	UB-50%RBA-FB	27.89	29.97					1045946	87.28	1.0	1.7	51.7	5.7	25.0	33.3	93.2	76.7	6667
	UB-50%RBA-HF	28.80																2667
	UB-70%RBA-FB	24.25	18.93					881757	87.08	2.7	3.3	64.7	2.7	60.0	100.0	81.9	62.5	2000
	UB-70%RBA-HF	28.33																1333
	UB-100%RBA	39.16	12.05					291291	82.50	16.3	3.3	60.3	20.3	55.0	70.0	51.8	42.3	1333

Notes: Basal area is for Douglas-fir only, and is interpolated between 1991 and 1994, after which it is assumed to have remained constant. Relative irradiance in 1994 and 1996 is assumed to have been a function of basal area (% irradiance = 30.113035 – 0.461306 basal area, $r^2 = 0.51$, $p = 0.0297$, $n = 9$), unless values so predicted are inconsistent with the basal area change observed in an individual treatment unit, in which case irradiance was kept constant for that unit. Seed germination and germinant survival values in 1993 are assumed to be the average of those observed in 1994, 1995, and 1996. Seedbeds: LM = live moss, FF = forest floor, DW = dead wood, MS = mineral soil, and US = unsuitable. WSI = water stress integral.

TABLE A3.2 *Summary of parameters influencing the natural regeneration of Douglas-fir over 3 years and their resulting predictions for germinant densities (procedure explained in Section 2.12)*

Seedling year, n	Treatment unit	Seedfall year n-1(per ha	% Seed predation	Seedbed distribution (% cover)				
				LM	FF	DW	MS	US*
t	(model abbreviations:)	f_{t-1}	p	c_1	c_2	c_3	c_4	
1993	BC-50%RBA-FB	275676	85.15	18.8	28.5	6.2	4.9	41.6
	BC-70%RBA-FB	91892	89.20	30.5	22.2	7.1	0.9	39.3
	BC-100%RBA	118919	81.71	46.6	23.2	1.0	0.0	29.2
	GL-50%RBA-FB	43243	81.28	8.0	24.9	6.3	2.7	58.1
	GL-70%RBA-FB	48649	99.58	14.3	38.7	4.2	1.8	40.3
	GL-100%RBA	32432	74.58	23.3	37.6	1.7	0.0	37.5
	UB-50%RBA-FB	10811	91.12	9.2	25.7	2.6	0.2	62.4
	UB-70%RBA-FB	78378	94.11	21.4	25.8	2.9	0.0	49.9
	UB-100%RBA	24324	82.15	21.8	54.7	0.7	0.2	22.7
1994	BC-50%RBA-FB	2759457	85.96	15.1	23.0	6.2	4.9	50.8
	BC-70%RBA-FB	2602700	89.60	26.7	19.4	7.1	1.6	45.2
	BC-100%RBA	3524321	76.85	42.7	21.2	1.9	0.1	34.1
	GL-50%RBA-FB	1289188	77.77	8.0	24.9	6.3	2.7	58.1
	GL-70%RBA-FB	1554053	96.76	14.3	38.7	4.2	1.8	40.3
	GL-100%RBA	1762160	74.72	23.3	37.6	1.7	0.0	37.5
	UB-50%RBA-FB	1359458	83.04	8.3	23.2	4.5	1.7	62.4
	UB-70%RBA-FB	1113512	86.70	19.6	23.6	4.9	2.0	49.9
	UB-100%RBA	1354053	70.83	16.2	40.5	3.0	0.8	39.5
1996	BC-50%RBA-FB	198198	90.28	15.0	22.8	6.2	4.9	51.1
	BC-70%RBA-FB	189189	88.00	26.6	19.4	7.1	1.6	45.4
	BC-100%RBA	89189	82.02	40.2	20.0	2.4	0.5	36.8
	GL-50%RBA-FB	945946	89.47	8.0	24.9	6.3	2.7	58.1
	GL-70%RBA-FB	772973	96.22	14.3	38.7	4.2	1.8	40.3
	GL-100%RBA	418919	76.63	23.3	37.6	1.7	0.0	37.5
	UB-50%RBA-FB	1045946	87.28	8.3	23.1	4.5	1.7	62.4
	UB-70%RBA-FB	881757	87.08	19.5	23.6	5.0	2.0	49.9
	UB-100%RBA	291291	82.50	16.1	40.3	3.1	0.8	39.7
(3 year)	50% RBA average	880880	85.71	11.0	24.6	5.4	2.9	56.1
(3 year)	70% RBA average	814789	91.92	20.8	27.8	5.2	1.5	44.5
(3 year)	100% RBA average	846179	78.00	28.2	34.7	1.9	0.3	34.9
Overall average:		847283	85.21	20.0	29.0	4.2	1.6	45.2
Correlation w/ obs. density:		0.69	-0.27	0.43	-0.18	-0.21	-0.16	-0.21

Notes: RBA = residual basal area; FB = logged by feller-buncher; HF = logged by hand-falling.

Abbreviations for variables are those portrayed in the model structure shown in Figure 2 and in the formula specified in Section 2.12.

Seedbeds: LM = live moss, FF = forest floor, DW = dead wood, MS = mineral soil, and US = unsuitable.

* US = unsuitable seedbeds; seed germination and germinant survival on these seedbeds is zero.

Germinant survival (%)				Predicted germinant density	Observed germinant density	Predicted minus observed		Predicted within 50%
LM	FF	DW	MS	(per ha)	(per ha)	(per ha)	Chi-square	of obs.?
v_1	v_2	v_3	v_4	r_i				
36.7	80.2	75.9	88.2	3650	1520	2130		over
51.4	81.6	79.0	55.8	1989	1747	242		equal
30.6	61.7	72.9	50.9	2910	6147	-3237		under
38.6	33.3	68.3	75.6	204	453	-249		under
63.9	67.9	79.1	65.2	4	120	-116		under
58.7	70.7	73.3	70.1	310	1587	-1277		under
12.5	66.7	66.9	76.0	9	760	-751		under
55.6	76.6	68.4	69.5	86	293	-207		under
25.6	31.9	30.0	41.7	96	120	-24	6891	equal
54.0	77.7	66.0	89.5	34412	61333	-26921		equal
50.5	82.8	77.9	78.0	50705	32000	18705		over
49.7	65.8	70.2	37.4	121823	406000	-284177		under
39.0	0.1	54.9	48.8	5726	19333	-13607		under
33.3	75.0	66.0	62.6	940	19333	-18393		under
71.5	100.0	60.9	63.4	17039	66000	-48961		under
0.1	100.0	32.0	78.3	2864	11333	-8469		under
50.0	75.0	80.0	65.0	2755	2000	755		equal
6.7	0.1	25.6	46.7	1623	8000	-6377	296751	under
33.5	90.0	69.7	92.3	1526	667	859		over
65.8	85.9	88.1	58.2	4933	6667	-1734		equal
69.2	57.6	83.2	67.9	3078	10667	-7589		under
25.0	100.0	97.7	97.9	3462	6000	-2538		equal
94.4	66.7	95.5	69.1	599	4667	-4068		under
35.7	66.7	88.3	85.1	1649	6000	-4351		under
25.0	33.3	93.2	76.7	3181	6667	-3486		under
60.0	100.0	81.9	62.5	4308	2000	2308		over
55.0	70.0	51.8	42.3	1746	1333	413	19344	equal
29.4	64.6	69.4	80.4	6115	12007	-5892	35586	
58.3	79.0	79.5	65.1	7369	7647	-279	35670	
47.0	58.3	61.8	56.2	16697	56206	-39509	251730	
44.9	67.3	70.2	67.2	10060	25287	-15227	322986	
0.09	0.03	-0.03	-0.33	0.94				

(4 overestimates)
(16 underestimates)
(7 within 50% of observed)